THE GENUS BRANCHIPODOPSIS (CRUSTACEA, BRANCHIOPODA, ANOSTRACA) IN SOUTHERN AFRICA. MORPHOLOGY, DISTRIBUTION, RELATIONSHIPS AND THE DESCRIPTION OF FIVE NEW SPECIES

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(With 41 figures and 1 table)

[MS accepted 27 January 1995]

ABSTRACT

The southern African species of *Branchipodopsis* are reviewed. Eleven previously known species are redescribed and five new species (*B. barnardi*, *B. dayae*, *B. drakensbergensis*, *B. hutchinsoni* and *B. underbergensis*) are described. The male second antennae (clypeus), cercopods, last abdominal segments and penes, as well as extensions of the genital segments of the females of certain species, are illustrated as are species distributions. The 16 species have been divided into groups based on a tentative cladistic analysis and a key, using the morphology of the clypeus, is presented. Intraspecific variation in two widespread species, *B. tridens* and *B. wolfi*, is illustrated and discussed. The characters used in the taxonomy of the genus *Branchipodopsis*, aspects of species diversity, habitats, dispersal and future research are commented on.

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INTRODUCTION

The anostracan family Branchipodidae is represented in Africa, Asia, Australia and Europe and is characterized by having the basal joints of the second antennae of the male fused to form a so-called 'clypeus'. In addition, according to Linder (1941), the genital segments of the male are negligibly swollen ventrally and there are no distinct seminal vesicles. The penes are close together, the basal parts are rigid and possess proximal outgrowths and usually distal ones as well. The retractable parts of the penes are armed with longitudinal rows of spines. The female ovisac is short and broad.

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Ann. S. Afr. Mus. 104 (10), 1996: 311-377, 41 figs, 1 table.

Initially, the family Branchipodidae Baird, 1852, included most of the known anostracan genera. Daday (1910) restricted the family to four genera, which he placed in two subfamilies: the Parartemiinae (which included the genus *Parartemia*), and the Branchipodinae (with three genera—*Branchipodopsis, Tanymastix* and *Branchipus*). This subfamilial distinction was based on the number of abdominal segments (eight in Parartemiinae and nine in Branchipodinae) and whether the cercopods articulated with the telson (Branchipus was later described by Masi (1925) and included in the family Branchipodidae. Barnard (1929) and Linder (1941) disputed Daday's division. Linder (1941) pointed out that both groups have eight abdominal segments and a telson, although the anterior boundary is almost obscure in *Parartemia*, and that the cercopods of this genus are as articulated as in the other genera. In addition, Linder (1941) placed little taxonomic value on the number of abdominal segments.

Linder (1941) provided a detailed synopsis of the family and stated that the degree to which the basal joints of the second antennae are joined varies from almost complete in Branchipus to the form where only the proximal halves are joined, as in those specimens of Branchipodopsis hodgsoni examined by him. He suggested that, in all of the Anostraca, it is difficult to decide the degree to which the basal joints must be fused to be called a clypeus and this presents some problems in determining the limits of the family Branchipodidae. Subsequent to Linder's (1941) monograph, few taxonomic contributions, apart from single species descriptions, have been made to the family. Brtek (1972) described a new genus, Tanymastigites, from North Africa and divided the Branchipodidae into three subfamilies, the Branchipodinae (Branchipodopsis, Branchipus and Parartemia), the Tanymastiginae (Tanymastix and Tanymastigites), and a third comprising the single genus, Metabranchipus. An indepth review of the family and the characters uniting the genera currently included in it is thus necessary. This is, unfortunately, beyond the scope of the present study, which focuses on southern African anostracans. Only the genus Branchipodopsis is represented in the region and it has been neglected, probably to an even greater extent than the other genera of the Branchipodidae.

Sars (1898) described the first Branchipodopsis species, B. hodgsoni, from Port Elizabeth, South Africa, and established the genus but he did not provide a generic diagnosis. Branchipus abiadi Brauer, 1877, a species from Rio de Oro, Mauritania in North West Africa, was later transferred to the genus Branchipodopsis by Linder (1941). Sars (1901) described Branchipodopsis affinis from Central Asia. In 1910, Daday described a further three species from southern Africa. In addition, he provided a diagnosis of the genus. He used the median ventral process, a small outgrowth from the anteroventral edge of the clypeus, the presence of two flat outgrowths on either side of it, and two more lamelliform and short outgrowths near the apical joints as diagnostic generic characters. Barnard (1929), however, in his review of the southern African phyllopods, suggested that the median ventral process is not always present; it may be present in some specimens of a species but not in others. Barnard (1929) provided illustrations, descriptions and locality data for then known southern African species, as well as for seven new species of *Branchipodopsis* from the region.

Linder (1941) provided additional data on *Branchipodopsis*, including details of the second maxilla, the structure and setation of the thoracopods, and the male genital segments and penes. He confirmed Barnard's (1929) comment on the median ventral process but suggested that it might be present in all specimens of a species but might have broken off in some. The proximal part of this structure is very narrow and could break without leaving any trace of its presence on the clypeus. Linder (1941) considered the lamelliform setiferous processes at the apical joint to be the most unique characteristic of *Branchipodopsis*, since these processes are not present in any other anostracans.

Subsequent to the work of Linder (1941), the genus *Branchipodopsis* has been neglected. A number of articles have been published on the Asian species *B. acanthopenes* (Mulhotra & Duda, 1970), *B. terpogossiani* Smirnov, 1936, and *B. affinis* (Roen 1952; Hartland-Rowe 1968; Tiwari 1972; Battish 1983; Brtek *et al.* 1984; Vechov 1988), but only two contributions have been made on the African representatives of the genus. Brehm (1958) illustrated, but did not name or provide detailed data of, one possible new species and other specimens that he identified as *B. karroensis* Barnard, 1929. These specimens, however, cannot be located and his identification is probably inaccurate. Loffler (1968) described *B. candea*, a new species from Mt Elgon in Central Africa, and provided data on *B. wolfi* Daday, 1910. Two recent publications (Hamer & Appleton 1991; Seaman *et al.* 1991) provided brief ecological information on *B. wolfi* and *B. tridens* Daday, 1910, respectively.

In southern Africa, sporadic collecting of Anostraca over the last 15 or so years and a more concentrated effort over the last four years have produced additional material of the genus *Branchipodopsis*. Examination of this has revealed the need to update Barnard's (1929) review in terms of distribution data, illustrations and descriptions, as well as to describe five new species. A key, based on the male clypeus, is provided and a division of the genus into groups based on cladograms is presented. The results of and problems associated with a cladistic analysis are outlined. Comments are made on the characters used for species identification and aspects of intraspecific variation, speciation, diversity, distribution and habitats are discussed.

MATERIALS AND METHODS

List of museums. The following abbreviations are used to indicate the museum collections included in this study: AM—Albany Museum, Grahamstown, South Africa; BMNH—British Museum of Natural History, London, England; HNHM—Hungarian Natural History Museum, Budapest, Hungary; USNM—National Museum of Natural History, Smithsonian Institution, Washington, U.S.A.; NM—Natal Museum, Pietermaritzburg, South Africa; SAM— South African Museum, Cape Town, South Africa; SMN—State Museum of Namibia, Windhoek, Namibia; TM—Transvaal Museum, Pretoria, South Africa; NMZ—National Museum, Bulawayo, Zimbabwe.

Material catalogued TM VLKE was collected on the Vernay-Lang Kalahari Expedition by the Transvaal Museum. Material catalogued under DB was collected by Dr T. Rutherford of the University of Lesotho and Dr J. A. Day of the University of Cape Town and was provided by Dr Denton Belk of Our Lady of the Lake University, Texas, U.S.A., from his personal collection.

Collecting. Hand-held dip nets of varying sizes and with mesh of 0.5-2.0 mm were used to collect anostracans. Specimens were preserved in 70 per cent ethanol or 4 per cent formalin. Dried pool sediment was collected from a number of localities for later rehydration in the laboratory. Hatched anostracans were cultured until mature enough to be identified.

Illustrations. Drawings were made using a Wild M-5 dissecting microscope or a Leitz Labor Lux 12 compound microscope and drawing tube. The clypeus was dissected from those species for which sufficient material was available, and cleaned and dehydrated in a graded ethanol series. Specimens were then critical point dried, mounted on stubs and coated with 20 nm of gold for scanning electron microscope observation using a Hitachi S-570 at an accelerating voltage of 10 or 12 kV. For some species, eggs were removed from the egg sac of females, rinsed in distilled water, oven-dried at 50°C for 24 hours, coated and viewed.

Measurements. Specimens of suitable quality were measured using a dissecting microscope and graticule. All measurements are presented as total body length (mean \pm standard deviation where n > 10, or as a range of lengths where n < 10), from the front of the head (excluding the clypeus) to the tip of the cercopods (excluding the setae) for sexually mature specimens.



Fig. 1. Diagram of idealized male second antennae (clypeus) illustrating terminology used in text and figures. Abbreviations: aj-apical joint; bj-basal joint; bp-basal process; c-clypeus; il-inner lobe; lp-lamelliform process; mvp-median ventral process; ol-outer lobe; pr-projection; tu-tubercle.

Terminology. The terminology used to describe the regions of the male clypeus is from Barnard (1929) and Linder (1941) and is illustrated in Figure 1. Each half of the clypeus (c) consists of a broad, stout basal joint (bj) and a slender, inwardly curved apical joint (aj). A lamelliform, setiferous process (lp) is present on the basal joint just proximal to the apical joint. The basal process (bp) is a somewhat flattened process situated anteriorly/anterodorsally on the basal joint. The basal process may have adjacent, apical lobes; these are termed the inner (il) and outer lobe (ol), which are rounded or conical structures of varying widths. Tubercles (tu) are smaller, digitiform projections that may be present apically or dorsally on the basal process. A smaller, acute projection (pr) may also be present near the apex of the basal process. The median ventral process (mvp) is a small, usually spinose, rounded or oval process, situated on the ventral surface in an anterior, median position on the basal joint. This structure is not present in all species.

Systematic analysis. Cladograms were initially drafted manually using Hennig augmentation, and were then generated using the 'mhennig', 'bb*' and 'ie-' commands of the program Hennig86. The following characters were used for the analyses: pair of spines on ventral surface of last abdominal segment; proportion of the cercopod inner margin with spines; cercopod shape; cercopod length in relation to body length; size of lamelliform process; curve of apical joint; distal inflation of posterior margin of apical joint; shape of the apex of the apical joint; presence of median ventral process; basal process shape; relative size of lobes of basal process; width of basal process in relation to height; presence of a dorsal tubercle on basal process; presence of a small projection on apex of inner lobe; large dorsal spinous projection at base of basal process. These were coded as binary characters, and it was assumed that the simplest form represented the primitive state. The genus *Parartemia* was used as the outgroup in the analysis.

The 16 species were divided into groups using a combination of the cladograms generated. Those species that were consistently grouped and that exhibit distinct similarities in the form of the clypeus were placed in the same group. This analysis and division must, however, for reasons discussed later, be considered as tentative.

DESCRIPTIONS

Class BRANCHIOPODA Latreille, 1817 Order ANOSTRACA Sars, 1867 Family **Branchipodidae** Baird, 1852

Genus Branchipodopsis Sars, 1898

Branchipodopsis Sars, 1898: 26. Daday, 1910: 293. Barnard, 1929: 192. Linder, 1941: 228. Eubranchinella Daday, 1910: 256. Mongolobranchipus Dybowski, 1927: 39.

Type species. Branchipodopsis hodgsoni Sars, 1898: 26, pl. 3.

Diagnosis

Males with basal joints of second antennae fused to form a clypeus. Each basal joint broad with a basal process in an anteromedian position and a setiferous lamelliform process distally. Apical joint slender and curved inwards. A median ventral process may be present (Fig. 1). Basal part of penes with rounded projection on median margin about halfway along length. Apical eversible part of penes with one longitudinal and a second, less regular row or scattered arrangement of spines (Fig. 2A-D). Thoracopods with a single preepipodite (Fig. 2E). Egg sac of female short and oval.

Typical morphology of labrum and maxillae is illustrated in Figure 3.



Fig. 2. A. Penes of Branchipodopsis wolfi (DB817). Ai. Ventral view of right penis; arrow indicates peg-like projection; 1—row of regular spinous processes; 2—irregular row of spinous processes. Aii. Dorsal view of right penis. B. Ventral view of right penis of B. wolfi (NMZ/Cr 6); arrow indicates peg-like projection; mp—median rounded projection.
C. Lateral view of right penis of B. wolfi (NMZ/Cr 6). D. Ventral view of right penis of B. natalensis (DB818). E. Right thoracopod 4 of B. tridens (AMLEN 150A). Scales: A-D = 1 mm; E = 0.5 mm.

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Branchipodopsis barnardi sp. nov. Figs 3-5

Material

Holotype. SAM-A40839, 1 \circ (13.9 mm); collected from rock pool (1.5 \times 2 m), 15 cm deep, Sehlabatebe National Park area, Drakensberg, Natal-Lesotho border, by M. Hamer and O. Wirminghaus, 23 April 1993.

Paratypes. SAM-A40840, 23 δ (14.8 \pm 1.0 mm), 44 \circ (15.5 \pm 1.5 mm); same collection data as holotype.

Other material examined. SAM-A40841, 1 & (14.6 mm), 2 \circ (15.0, 15.3 mm); collected from type locality, by O. Wirminghaus and H. Adie, 11 April 1993.



Fig. 3. Mouthparts of male *Branchipodopsis barnardi* sp. nov. (SAM-A40840, paratype).
A. Dorsal view of maxilla I. B. Distal setae of maxilla I: i-lateral view; ii, iii-dorsal view of portion of setae (position indicated by arrow on Fig. 3A) showing variation in shape of scale-like structure detail of setae on maxilla I. C. Maxilla II. D. Lateral view of labrum.
E. Dorsal view of labrum. Scales: A, E = 0.1 mm; B, C = 0.05 mm; D = 0.05 mm; C = 0.5 mm.



Fig. 4. Branchipodopsis barnardi sp. nov. (SAM-A40840, paratype). A. Clypeus.
B. Dorsal view of cercopods of male. C. Ventral view of posterior region of abdomen; arrow indicates spine. D. Ventral view of basal part of penes; arrow indicates median projection. E. Lateral view of genital segments of female showing egg sac and bulbous processes (indicated by arrow). F. Dorsal view of female antenna. G-I. Basal processes of three specimens illustrating intrapopulation variation in shape of apical region.

Scales = 0.5 mm.

Description of male

Clypeus. Basal process long and slender. Apical region with digitiform inner lobe and short, flat outer lobe (Figs 4A, 5A-B). Reticulate patterning on dorsal proximal surface of basal process (Fig. 5C). Lamelliform process long, prominent and elliptical in shape with long sparse setae (Fig. 4A). Apical joint slender, distal third weakly curved inwards and apex blunt (Figs 4A, 5A). Median ventral process absent.

Cercopods. Moderate length (ratio to body length about 0.2:1). Proximally stout, tapering distally and with outer margins weakly convex (Fig. 4B). Short to medium length setae on outer margins, replaced by three spines distally. Inner margins with small patch of sparse setae proximally, followed by 12–15 evenly spaced spines (Fig. 4B).

Abdominal spines. Pair of short, stout and blunt spines present on ventral surface of last abdominal segment (Fig. 4C).

Penes. Basal part short and stout, with proximal region bulbous and with indistinct rounded projection on inner margin (Fig. 4D).

Description of female

Thoracic segments. Last thoracic segment with pair of obvious, rounded and bulbous extensions dorsally (Fig. 4E).

Antenna. Apical point on second antenna almost one-half length of antenna (Fig. 4F).

Egg morphology

Surface of egg with irregularly shaped, five-sided depressions separated by high rounded ridges (Fig. 5D).

Differential diagnosis

Branchipodopsis barnardi is easily distinguished from all other species of the genus by the large elliptical lamelliform process, the slender apical joint and the long, digitiform and distally bilobed shape of the basal process.

Distribution

Branchipodopsis barnardi has, to date, only been collected from rock pools in the high-altitude (2000 m) Drakensberg region, on the border of Sehlabatebe National Park in Lesotho and the Bushman's Nek area of Natal (Fig. 39).

Remarks

In the cladograms presented in Figure 41, *B. barnardi* did not show a close relationship with any of the other species. As a result of the simple structure of the basal process and shape of the apical joint, the position of *B. barnardi* on this cladogram suggests a primitive form. *Branchipodopsis barnardi* does, however, share certain characters with *B. drepane* Barnard, 1929. Both species have slender bilobed basal processes, with a smaller outer lobe, and the apical joint is smooth and weakly curved. For these reasons, *B. barnardi* and *B. drepane* have been included in the same group (see Table 1).

The colour of live specimens varied according to the pool from which they were collected. One population (used for DNA extraction) was a pale orangered colour before preservation, whereas the type specimens were a pale aqua blue. The labral area and a thin stripe along the gut region were red in all specimens. There was also some degree of intrapopulation variation in the shape of the apex of the basal process as illustrated (Fig. 4G–I).

Etymology

Branchipodopsis barnardi is named for the late Dr K. H. Barnard, of the SAM, who was the author of the first review of the southern African 'Phyllopoda' in 1929 and who collected a large number of specimens currently housed in that institution.



Fig. 5. Branchipodopsis barnardi sp. nov. (SAM-A40840, paratype). A. Dorsal view of clypeus. B. Basal processes; il—inner lobe; arrow indicates position of outer lobe. C. Apical region of left basal process showing reticulate patterning. D. Egg. Scales: A-B = 0.5 mm; $C-D = 100 \ \mu\text{m}$.

Branchipodopsis browni Barnard, 1924 Figs 6-7

Branchipodopsis browni Barnard, 1924: 217, pl. 26 (fig. 4); 1929: 198, fig. 5a.

Material

Syntypes. SAM-A6705, large number of specimens, 24 \circ measured (12.0 \pm 0.7 mm), 26 \circ measured (13.3 \pm 0.6 mm); collected from Kalkfontein South, Great Namaqualand, Namibia, by J. S. Brown, date unknown.

Other material examined. SAM-A7600, 7 \diamond (13.1-15.6 mm), 4 \heartsuit (17.5-20.0 mm); collected from Williston, Cape Province in 1939, collector unknown. AM LEN 79B, 6 \diamond (11.8-13.0 mm), 7 \heartsuit (13.1-14.8 mm); collected from a large (20 \times 30 m), shallow (20-35 cm) turbid pool, sparsely vegetated with grass, 10 km south of Carnarvon on the road to Loxton, Karoo, Cape Province, by M. Hamer, 16 February 1990. AM LEN 164A, 3 \diamond (6.6, 8.0, 8.1 mm), 1 \heartsuit (6.9 mm); hatched from dried sediment collected 8 km north-east of Fraserburg, Karoo, Cape Province, by M. Hamer, 6 January 1993. AM 614/93, 1 \diamond (14.2 mm), 1 \heartsuit (16.5 mm); collected from inundated area along road, 8 km from Richmond, by K. Martens, 6 April 1993.

Redescription of adult male

Clypeus. Basal process conical proximally, apically inflated and bluntly rounded, with a series of short denticles on apex (Figs 6A, 7A-C). A distal, anteriorly curved and pointed projection on inner margin of basal process (Fig. 7B-C). One or two small, acute projections dorsomedially near apex of basal process (Fig. 7B-C). Lamelliform process very large (as long as basal process) and oval (Fig. 6A). Apical joint slender, long, smooth and curved inwards with apex slightly inflated and blunt (Fig. 6A). Median ventral process large (approximately one-half length of basal process), oval and spinose (Figs 7A, 8A).

Cercopods. About one-fifth of body length, margins straight, with long, plumose setae along outer margins and proximal two-thirds of inner margins. Distal third of inner margins with 6-8 widely spaced, long spines (Fig. 6B).

Abdominal spines. Two small ventral spines on last abdominal segment (Fig. 6C).

Penes. Median projection bluntly rounded and prominent. Distal region of basal part with small but distinct peg-like projection on outer margin (Fig. 6D).

Remarks

Barnard (1924) stated that *B. browni* closely resembles *B. hodgsoni* but that the presence of abdominal spines in the former species separates them. The arrangement of the basal process and associated projections is, however, quite distinct in these two species. In the cladogram (see Fig. 41), *B. browni* was positioned closest to *B. wolfi*. These two species have an apical projection on unlobed or unilobed basal processes and distinctly bent apical joints.

Variation in the size of the dorsomedian projection of the basal process and the apical denticles is illustrated in Figure 7B and C.



Fig. 6. *Branchipodopsis browni*. A. Dorsal view of clypeus (AMLEN 79B). B. Cercopods of male (AMLEN 79B). C. Ventral view of last abdominal segment of male (SAM-A6705, syntype); arrow indicates spine. D. Ventral view of right penis with apical region extended (SAM-A6705); arrow indicates peg-like projection. E. Female second antenna (SAM-A6705). Scales = 0.5 mm.

Distribution

Branchipodopsis browni has only been reported from the above five localities in the arid southern Namibian and Karoo regions (Fig. 38).



Fig. 7. Branchipodopsis browni. A. Basal processes and median ventral process of AM LEN 164A specimen. B. Detail of apex of left basal process; arrow indicates median, dorsal projection. C. Detail of left basal process of AM LEN 79B specimen; arrow indicates small median, dorsal projection. Scales: $A = 150 \mu m$; $B = 50 \mu m$; $C = 100 \mu m$.

Branchipodopsis dayae sp. nov. Figs 8-9

Material

Holotype. SAM-A40842, 1 & (17.3 mm); collected Eland's Bay, Cape Province, by J. Lighton, 23 November 1980.

Paratypes. SAM-A40843, 2 ♂ (15.3, 16.9 mm), 2 ♀ (12.8, 14.4 mm); collection data as for holotype.

Other material examined. SAM-A40849, 1 &, in poor condition; hatched in laboratory from sediment collected from dry depression on roadside, Koppieskraal Pan, approximately 36 km from Namibian border on R31, Cape Province, by M. Hamer, 22 December 1992.



Fig. 8. Branchipodopsis dayae sp. nov. (SAM-A40843, paratype). A. Dorsal view of clypeus; arrow indicates small projection on apical, median margin of basal process.
B. Cercopods of male. C. Ventral view of penes. D. Median view of apical, everted part of penes; arrow indicates blunt, peg-like projection. Scales = 0.5 mm.

Description of male

Clypeus. Basal process broad and apically bilobed. Outer lobe rounded, inner more conical, with small acute projection apically on median margin (Figs 8A, 9A-B). Lamelliform process small and round (Fig. 8A). Apical joint weakly curved inwards, distal region foot-shaped (Figs 8A, 9A, C). Median ventral process small, round and with short, blunt spines (Fig. 9D).



Fig. 9. Branchipodopsis dayae sp. nov. (SAM-A40843, paratype). A. Dorsal view of clypeus. B. Apical region of left basal process (arrow indicates small projection on inner lobe). C. Distal region of apical joint. D. Dorsal view of median ventral process. Scales: A = 0.5 mm; B-C = 100 μ m; D = 50 μ m.

Cercopods. Moderate length (ratio to body length approximately 0.25:1), outer margins weakly convex and with short setae along almost entire length except distal region where these replaced by 3-5 widely spaced, short spines (Fig. 8B). Proximal fifth of inner margins with short setae and remainder of length with 12 short spines (Fig. 8B).

Abdominal spines. A pair of blunt spines present on ventral surface of last abdominal segment.

Penes. Basal part stout, inner margin with distinct conical projection proximally and lateral margin with indistinct peg-like projection distally (Fig. 8C-D).

Differential diagnosis

The distal region of the apical joint and the shape of the two lobes of the basal process of B. dayae are unique to this species. Branchipodopsis drepane also has characteristic apical joint apices but these are hook-shaped rather than

foot-shaped. This species also shares the small, rounded lamelliform processes with B. dayae but the basal processes of the two species are clearly different. The basal process morphology of B. dayae resembles that of B. karroensis Barnard, 1929, and these two species were shown to be closely associated by the cladistic analyses (Fig. 41).

Distribution

Branchipodopsis dayae has been collected from Eland's Bay on the Cape west coast and from the Gordonia region between Namibia and Botswana (Fig. 40). It is possible that this species also occurs in other waterbodies in the area between these two localities.

Etymology

Branchipodopsis dayae is named after Dr J. A. Day of the University of Cape Town, who has contributed to the knowledge of temporary waterbodies in southern Africa. She also collected numerous Anostraca and kindly made her collection, including the type specimens of this species, available for study.

Branchipodopsis drakensbergensis sp. nov.

Figs 10-13

Material

Holotype. SAM-A40834, δ (12.5 mm); collected from small (40 × 50 cm) rock pool in boulder, 15 cm deep, Loteni Nature Reserve, Drakensberg, Natal, by M. Hamer, 6 January 1992.

Paratypes. SAM-A40835, 14 d (12.6 \pm 0.5 mm), 5 \circ (11.9-12.8 mm); same collection data as holotype specimen.

Other material examined. SAM-A40836, 17 \diamond (11.1 \pm 0.5 mm), 34 \heartsuit (10.4 \pm 0.5 mm); collected from small pool (30 \times 40 cm) in boulder, 10 cm deep, Loteni Nature Reserve, Drakensberg, Natal, by M. Hamer, 6 January 1992. AM LEN 158A, 7 \diamond (7.5-10.5 mm), 5 \heartsuit (9.0-18.1 mm); collected in rock pool on top of Prentjiesberg, Farm Montana, Ugie, Cape Province, by R. McC. Pott, 4 April 1991. AM LEN 159A, 12 \diamond (2 with damaged cercopods, remainder 13.1-13.9 mm), 4 \heartsuit (12.3-14.0 mm); locality as for AM LEN 158A; collected by R. McC. Pott, 22 January 1992. SAM-A11593, 4 \diamond (9.4-12.0 mm), 5 \heartsuit (10.0-11.3 mm); collected from Giant's Castle, Drakensberg, Natal, by Ewer, 1951. AM REA 77A, 12 \diamond (8.9 \pm 0.6 mm), 26 \heartsuit (9.1 \pm 0.8 mm); collected from temporary vlei at Witkoppies, Benoni, Transvaal, by P. A. Reavell, 31 April 1971.

Description of male

Clypeus. Basal process slender, distally bilobed, with inner lobe twice as long as outer, both apically narrow and rounded (Figs 10A, 11A–B). Inner lobe with 1–2 small projections medianly on apex (Fig. 12A–C). Large spinous projection proximally on dorsal surface of basal process (Figs 10B–C, 11A–C), one-half to two-thirds length of basal process and with apical denticles or scales



Fig. 10. *Branchipodopsis drakensbergensis* sp. nov. A. Dorsal view of clypeus (SAM-A40835, paratype). B. Lateral view of basal process of Loteni specimens (SAM-A40835). C. Lateral view of basal process of Ugie specimen (AMLEN 159A); il—inner lobe; ol—outer lobe; s—spinous projection. D. Cercopods of male (SAM-A11593). E. Ventral view of basal part of penes (SAM-A40835). F. Lateral view of genital segments of female (AMLEN 159A) showing egg sac. G. Female antenna (AMLEN 159A). Scales = 0.5 mm.

(Fig. 13A-C). Median ventral process prominent, ovate and with long spines distally (Figs 10A, 11B). Lamelliform process ovate, with long setae (Figs 10A, 11C). Apical joint strongly curved inwards with rounded apices (Fig. 10A).

Cercopods. Moderate length (ratio to body length approximately 0.25:1). Outer margins strongly convex, with setae along entire length. Patch of setae on

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proximal fifth of inner margins, followed by 17-19 evenly spaced spines (Fig. 10D).

Abdominal spines. A pair of prominent spines on last abdominal segment.

Penes. Basal part long, with distinct, round projection about halfway along inner margin (Fig. 10E).

Egg morphology

Eggs with deeply crumpled appearance created by irregular narrow depressions separated by high ridges (Fig. 13D). Surface of eggs roughened with numerous small lumps.





Fig. 11. Branchipodopsis drakensbergensis sp. nov. A. Dorsal view of basal processes of clypeus, Loteni specimen (SAM-A40835, paratype); outer lobe of left basal process not visible; arrow indicates outer lobe of right basal process; s—spinous projection. B. Basal processes of Ugie specimen (AM LEN 159A); arrow indicates median ventral process. C. Left basal process of Benoni specimens (AMREA77A); lp—lamelliform process.

Differential diagnosis

Branchipodopsis drakensbergensis resembles B. tridens in the presence of a dorsal projection on the basal process and the bilobed basal process. However, the prominent median ventral process, absent or vestigial in B. tridens, and the distinctly slender basal process as opposed to the broad shape of these structures in B. tridens, separate the two species. As a result of this similarity, the Giant's Castle specimens (SAM-A11595) were previously labelled as B. tridens in the SAM collection.



Fig. 12. Branchipodopsis drakensbergensis sp. nov. A. Detail of apex of inner lobe of basal process, Loteni specimen (SAM-A40835, paratype). B. Detail of apex of inner lobe of basal process, Ugie specimen (AM LEN 159A). C. Detail of apex of inner lobe of basal process, Benoni specimen (AM REA 77A). Scales: $A-B = 10 \mu m$; $C = 50 \mu m$.



Fig. 13. Branchipodopsis drakensbergensis sp. nov. A. Basal process, illustrating apex spinous process (indicated by arrow), Loteni specimen (SAM-A40835, paratype). B. Detail of apex of spinous process, Ugie specimen (AM LEN 159A). C. Detail of apex of spinous process, Benoni specimen (AM REA 77A). D. Egg. Scales: A, D = 100 μ m; B = 50 μ m; C = 10 μ m.

Distribution

Branchipodopsis drakensbergensis occurs in high-altitude rock pools in the southern and central Drakensberg. The single Transvaal locality could indicate a wider distribution for this species as well as a wider habitat range (Fig. 39).

Remarks

There is some variation in clypeus morphology between populations from different localities. For example, the specimens from Loteni have a flattened, spatulate process on the apex of the inner lobe of the basal process as opposed to a pointed one in the specimens from Benoni and Ugie (Fig. 12A-C) and there is a slight difference in the shape of the basal process and spinous projection (Fig. 10B-C). The latter projection has long extensions apically in the Loteni specimens (Fig. 13A), whereas these are flattened and scale-like in the specimens from Benoni (Fig. 13C) and somewhat intermediate in those from Ugie (Fig. 13B). In addition, the cercopods of the Benoni specimens have fewer spines (9) on the inner margin than the specimes from the Drakensberg. These differences could indicate two distinct species but, in the light of the large amount of interpopulation variation in other widespread species of the genus and because of the overall similarity in clypeus shape, a single species has been described.

In terms of relationships to other species of the genus, B. drakensbergensis could be related to B. tridens, since both species have a spinous projection on the basal process and bilobed basal processes. However, the cladograms (Fig. 41) do not indicate this relationship and the spinous projection could be a homoplasious character.

Etymology

Branchipodopsis drakensbergensis is named after the mountain range from which most of the material was collected.

Branchipodopsis drepane Barnard, 1929 Fig. 14

Branchipodopsis drepane Barnard, 1929: 199, fig. 5e-f.

Material

Holotype. SAM-A7259, 1δ (12.4 mm), distal part of right apical joint damaged; collected from Great Fish River, near Gibeon, Namibia, by R. W. Tucker, date unknown.

Other material examined. BMNH 1932.2.25.41, 1 ♂ (12.3 mm); same locality and collection data as type specimen.

Redescription of adult male

Clypeus. Basal process long and slender with distinct indentation about halfway along lateral margin. Distally, basal process with a smaller outer lobe and a higher and larger, rounded inner lobe (Fig. 14A). Lamelliform process small, slender and oval (Fig. 14A). Apical joint weakly curved inwards, with hook-shaped, acute apex (Fig. 14A). Median ventral process obovate, apically flat and with surface covered by small spines (Fig. 14B).

Cercopods. Ratio to body length approximately 0.26:1, slender, and with outer margins only slightly convex. Outer margins and proximal half of inner

margins with plumose setae. Distally, inner margins with six large, widely spaced spines (Fig. 14C).

Abdominal spines. Last abdominal segment with two stout, blunt spines on ventral surface.

Penes. Proximal region of basal part with obscure bulge on lateral surface, followed by small rounded projection on median margin (Fig. 14D).

Distribution

Branchipodopsis drepane has only been collected from the type locality in southern Namibia (Fig. 38).



Fig. 14. Branchipodopsis drepane (BMNH 1932.2.25.41). A. Dorsal view of clypeus; il-inner lobe; ol-outer lobe. B. Ventral view of basal processes and median ventral process. C. Cercopods of male. D. Ventral view of basal part of penes; arrows indicate lateral and median proximal projections. Scales = 0.5 mm.

Branchipodopsis hodgsoni Sars, 1898 Figs 15-16

Branchipodopsis hodgsoni Sars, 1898: 26, pl. 3 (figs 1-9). Daday, 1910: 301, fig. 51. Barnard, 1929: 194, fig. 5k-l. Branchipodopsis braueri Pesta, 1921: 94.

Material

Syntypes. SAM-A1488, $1 \circ (11.6 \text{ mm})$, $1 \circ \text{with damaged abdomen and cercopods; hatched from dried sediment collected from Port Elizabeth, Cape Province, by J. V. Hodgson, May 1897.$

Other material examined. SAM-A6721, 14 \circ (14.0 \pm 1.3 mm), 4 \circ (10.5-16.5 mm); collected from Ashton, Cape Province, collector unknown, 27 August 1910. SAM-A13631, 1 \circ (11.9 mm), 5 \circ (8.8-14.4 mm); collected from freshwater pool, Kenton-on-Sea, Cape Province, by R. A. Jubb, April



Fig. 15. Branchipodopsis hodgsoni. A. Dorsal view of clypeus (HNHM I/A-76); arrows indicate dorsal and ventral lobes of basal process. B. Basal processes and median ventral process of AM LEN 149A specimen; 1—dorsal lobe; 2—ventral lobe. C. Lateral view of basal process (AM LEN 149A). D. Cercopods of male (SAM-A6721). E. Ventral view of basal part of right penis (AM LEN 149A); arrow indicates peg-like process. F. Female second antenna (SAM-A6721). Scales = 0.5 mm.

1963. AM 107A, 1 \diamond with right half of clypeus damaged (9.2 mm), 1 \diamond (10.4 mm); same collection data as SAM-A13631. HNHM I/A-76, 1 \diamond (11.8 mm), 1 \diamond (8.3 mm); data as for syntypes. AM LEN 149A, 7 \diamond (6.3-12.6 mm); collected from a shallow (5-10 cm), clear stretch of water with sparse, dead vegetation on side of main road from Bredasdorp to Struisbaai, Cape Province, by M. Hamer, 17 July 1990.

Redescription of adult male

Clypeus. Basal process with broad, double-lobed base; second lobe positioned slightly ventral to first (Figs 15A-C, 16A). Narrow, medianly directed apex with two small pointed tubercles (Figs 15A, 16A). Lamelliform process oval and slender (Fig. 15A). Apical joint strongly curved, with distinct bend and blunt apex (Fig. 15A). Median ventral process large, oval and with blunt spines (Fig. 16B).

Cercopods. Moderate length (ratio to total body length approximately 0.24:1). Outer margins convex with short plumose setae along entire length. Proximal two-fifths of inner margins with plumose setae, followed by 8-10 acute, evenly spaced spines (Fig. 15D).

Abdominal spines. Last abdominal segment without ventral spines.

Penes. Basal part with large rounded projection on median margin and small, but distinct, peg-like projection distally on lateral margin (Fig. 15E).

Distribution

Branchipodopsis hodgsoni appears to be concentrated in the south-east coastal region of South Africa, from Kenton-on-Sea in the north to Bredasdorp in the south. The locality of Ashton in the western Cape represents the furthest inland record (Fig. 38).



Fig. 16. Branchipodopsis hodgsoni (AM LEN 149A). A. Right basal process; 1-dorsal lobe; 2-ventral lobe. B. Dorsal view of median ventral process. Scales: A = 50 μm; B = 25 μm.

Remarks

Branchipodopsis hodgsoni is quite distinct from the other species of the genus in that the basal process has a bilobed appearance, with one lobe ventral to the other. This double-lobed arrangement is not always as evident as illustrated but this is usually a result of the preservation of the specimens. The two small apical tubercles on the dorsal lobe are also unique to *B. hodgsoni*.

Branchipodopsis hutchinsoni sp. nov. Figs 17-18

Material

Holotype. SAM-A40844, 1 δ (12.3 mm); collected from heavily vegetated roadside ditch (30 × 1 m), 20-30 cm deep, 30 km along dirt road from Hutch-inson to Richmond, Karoo, Cape Province, by M. Hamer, 16 February 1990.

Paratypes. SAM-A40845, 18 \circ (12.0 \pm 0.7 mm), 32 \circ (11.4 \pm 0.8 mm); collection data as for holotype.

Description of male

Clypeus. Basal process broad, apically bilobed, lobes subequal, roundedconical, with inner lobe slightly more conical than outer (Figs 17A, 18A-B). Inner lobe with small, acute process on median, apical surface (Fig. 18B). A medianly directed, conical tubercle on dorsal surface at base of inner lobe (Fig. 18A-C). Lamelliform process obovate, with setulose scalloped margin (Fig. 17A). Apical joint with distinct inward bend, apically blunt and broad (Fig. 17A). Median ventral process prominent, ovate and with short spines (Fig. 17A).

Cercopods. Moderate length (ratio to body length approximately 0.25:1), outer margins strongly convex with medium length setae along four-fifths of length, distal fifth with 3-6 short spines. Inner margins with patch of setae on proximal quarter, followed by 12-16 strong spines (Fig. 17B).

Abdominal spines. A small blunt spine present medianly at the base of each cercopod. A pair of rounded processes present ventrally on penultimate segment (Fig. 17C).

Penes. Basal part slender with small rounded projection proximally on median margin and a narrow, peg-like projection apically on lateral margin (Fig. 17D).

Egg morphology

Surface of egg with mildly crumpled appearance created by three- to fivesided depressions separated by broad ridges with sharp crests (Fig. 18D).

Differential diagnosis

Branchipodopsis hutchinsoni, B. karroensis, B. dayae and B. natalensis Barnard, 1929, all have broad bilobed basal processes with both lobes of approximately equal size. The inner lobe of both B. karroensis and B. dayae also has a small apical projection but neither species has a dorsal tubercle such as that of *B. hutchinsoni* and *B. natalensis*. The latter two species can be separated by the rounder shape of the basal processes, the strongly curved cercopods and the scalloped lamelliform processes of *B. hutchinsoni*.

Distribution

Branchipodopsis hutchinsoni has, to date, only been collected from the type locality in the Karoo (Fig. 39).



Fig. 17. Branchipodopsis hutchinsoni sp. nov. (SAM-A40845, paratype). A. Dorsal view of clypeus; arrow indicates small projection on apex of inner lobe. B. Cercopods of male.
C. Ventral view of posterior region of abdomen showing rounded projections on penultimate segment (indicated by large arrows) and blunt spinous processes (indicated by small arrows).
D. Ventral view of genital region of male showing basal parts of penes; arrows indicate proximal median process and distal lateral process. E. Dorsal view of genital segments of female showing absence of outgrowths in this region. F. Female second antenna.

Scales = 0.5 mm.



Fig. 18. Branchipodopsis hutchinsoni sp. nov. (SAM-A40845, paratype). A. Dorsal view of basal processes of clypeus. B. Detail of right basal process. C. Detail of apex of median dorsal projection on basal process. D. Egg. Scales: A-B, $D = 100 \ \mu m$; $C = 10 \ \mu m$.

Etymology

Branchipodopsis hutchinsoni is named in honour of the limnologist Professor Evelyn Hutchinson, in memory of his contributions to the knowledge of freshwater habitats.

> Branchipodopsis kalaharensis Daday, 1910 Figs 19-20

Branchipodopsis kalaharensis Daday, 1910: 296, fig. 49. Barnard, 1929: 194, fig. 5j; 1935: 487.

Material

Syntypes. 2 δ and 2 \circ housed in the Senckenberg Museum; collected from the Kalahari, by D. Schultze, date unknown (Daday 1910).

Material examined. SAM-A11594, 2 δ , 1 with damaged cercopods (other 11.2 mm), 6 \circ (10.0-13.5 mm); collected from Kanke Pan (90 miles west of Molepole), Botswana, by the Vernay-Lang Kalahari Expedition, 19 March 1930. TM VLKE94, 8 δ (10.0-14.0 mm); same collection data as SAM-A11594. TM VLKE460a, 8 δ (10.6-12.8 mm); collected from Sunnyside, Botswana, by the Vernay-Lang Kalahari Expedition, 20 April 1930.

Redescription of adult male

Clypeus. Basal process broad, apically bilobed with a narrow conical inner lobe and an outer, less prominent but similarly shaped lobe (Figs 19A, 20A-B). Lamelliform process narrow and oval (Fig. 19A). Apical joint strongly curved inwards and with distinct bend (Figs 19A, 20A). Median ventral process absent or obscure.

Cercopods. Long (ratio to body length approximately 0.3:1), with proximal two-thirds of outer margins convex and with plumose setae of moderate length. Distal third of outer margins with 8–10 widely spaced, spiniform setae. Proximal quarter of inner margins with plumose setae, followed by approximately 15 regularly spaced, strong spines (Fig. 19B).



Fig. 19. Branchipodopsis kalaharensis (TM VLKE94). A. Dorsal view of clypeus; il—inner lobe; ol—outer lobe. B. Cercopods of male. C. Ventral view of basal part of left penis; arrow indicates blunt apical projection. Scales = 0.5 mm.

Abdominal spines. Last abdominal segment without ventral spines.

Penes. Basal part with large rounded projection on proximal region of median margin and obscure blunt projection on apex of lateral margin (Fig. 19C).

Remarks

Daday (1910) attributed *Branchipodopsis kalaharensis* to Wolf, who initially examined the type material. The description by Wolf was, however, never published (Forró & Brtek 1984).



Fig. 20. Branchipodopsis kalaharensis (TM VLKE 94). A. Dorsal view of clypeus. B. Detail of right basal process. Scales: A = 0.5 mm; $B = 100 \mu$ m.

Daday (1910) suggested that, because of the simple structure of the basal process of this species, the other species of the genus are derived from it. Of the five species that had been described at that stage, Daday named the Indian species *B. affinis* as the closest relative of *B. kalaharensis*. In southern Africa, there are a number of species that have bilobed basal processes but the lobes in these species are much rounder than in *B. kalaharensis*. It is, however, quite possible that the simple bilobed shape of the basal process of *B. kalaharensis* does represent the ancestral form for species such as *B. dayae*, *B. hutchinsoni*, *B. karoensis* and *B. natalensis*. This is not reflected by the cladistic analyses (Fig. 41), where *B. kalaharensis* was linked to *B. simplex* Barnard, 1924, which has an unlobed basal process, but has apical joints of similar shape and also lacks a distinct median ventral process.

Distribution

Branchipodopsis kalaharensis has only been collected from central Botswana (Fig. 38).

Branchipodopsis kaokoensis Barnard, 1929

Fig. 21

Branchipodopsis kaokoensis Barnard, 1929: 200, fig. 5q.

Material

Barnard (1929) stated that the type material, consisting of one male and four females, was housed in the SAM but this could not be located. The collection data and catalogue number of four specimens in the BMNH suggest that these are the types supposedly in the SAM. Barnard (1929) gave the length as 13 mm, but his measurements did not include cercopods and this could account for the difference in measurements presented here, or he could have presented an average length for all five specimens. Details for these specimens are as follows: BMNH 1932.2.25.42-45, 1 σ with left half of clypeus removed (21.0 mm), 1 \circ (13.5 mm); collected from Choabendus (115 miles north-west of Outjo), Kaokoveld, Namibia, by K. H. Barnard, date unknown.

Redescription of adult male

Clypeus. Basal process broad, apically trilobed with inner lobe digitiform, the outer lobe similarly shaped but more acute and the median lobe the largest and apically flattened. A long, conical, spiniform projection present dorsally at proximal region of basal process (Fig. 21A). Lamelliform process narrow and ovate. Apical joint stout, curved inwards and apically deeply bifid. A short, spiniform projection on dorsal surface approximately midway along apical joint, followed by a larger, triangular projection ventrolaterally just proximal to apex (Fig. 21A). Median ventral process absent.

Cercopods. Moderate length (ratio to body length approximately 0.26:1), slender and with outer margins slightly convex. Outer margins with moderately long plumose setae along about half of length, followed by 5–6 small, sharp spines. Inner margins with plumose setae along proximal quarter of length, followed by 15 prominent spines (Fig. 21B).

Abdominal spines. Last abdominal segment with two large, broad spines on ventral surface (Fig. 21C).

Penes. Basal part short and broad without distinct median projections.

Remarks

The penes of the single specimen examined could be shrunken by the preservative since they look different to those of other species of the genus.

Barnard (1929) remarked on the similarity between *B. kaokoensis* and *B. tridens*, but stated that no *B. tridens* specimens had any hint of projections on the apical joint of the clypeus. However, the two species were consistently very closely linked in the cladistic analyses (Fig. 41) and there is little doubt that *B. kaokoensis* and *B. tridens* represent advanced, closely related forms.

Distribution

Branchipodopsis kaokoensis has only been recorded from the type locality in Namibia (Fig. 38).



Fig. 21. Branchipodopsis kaokoensis (BMNH 1932.2.25.42-45). A. Dorsal view of clypeus; arrows indicate projections on apical joint. B. Cercopods of male. C. Ventral view of last abdominal segment of male. Scales = 0.5 mm.

Branchipodopsis karroensis Barnard, 1929 Fig. 22

Branchipodopsis karroensis Barnard, 1929: 198, fig. 5m-n.

Material

Syntypes. SAM-A5919, 2 $\stackrel{\circ}{\circ}$ (9.8 mm; 12.0 mm), 5 $\stackrel{\circ}{\circ}$ (9.5-12.3 mm); collected from Hoogeveld, south-west of Beaufort West, Cape Province, by S. H. Haughton, date unknown.

Other material examined. BMNH 1932.2.25.36-40, $1 \circ (10.0 \text{ mm})$, $1 \circ (11.3 \text{ mm})$; data as for syntypes.

Redescription of adult male

Clypeus. Basal process broad. Apex with two rounded lobes and a small acute process on the median margin of inner lobe. Lamelliform process oval. Apical joint curved inwards with slight inflation just proximal to blunt apex. Median ventral process with broad base and narrower distal region (Fig. 22A).

Cercopods. Long (ratio to body length approximately 0.30:1). Outer margins weakly convex, and with setae along almost entire length. Distal region



Fig. 22. Branchipodopsis karroensis. A. Dorsal view of clypeus (SAM-A5919, syntype); arrow indicates projection on median margin of inner lobe. B. Cercopods of male (BMNH 1932.2.25.36-40). C. Left penis with apical region partially extended (SAM-A5919); arrows indicate rounded projection on median margin and peg-like projection on lateral margin. D. Female second antenna (SAM-A5919). Scales = 0.5 mm.

with three spines. Proximal half of inner margins with widely spaced, short setae followed by 8-9 spines (Fig. 22B).

Abdominal spines. Ventral surface of last abdominal segment with two short but strong spines.

Penes. Basal part with distinct, rounded projection proximally on median margin and prominent peg-like projection apically on lateral margin (Fig. 22C).

Description of female

Second antenna. Apical pointed process long (one-half the length of antenna) (Fig. 22D).

Distribution

Branchipodopsis karroensis has only been recorded from the type locality in the Karoo (Fig. 38).

Remarks

Brehm (1958) identified specimens from Blouberg in the Transvaal as *B. karroensis* but this record is considered invalid, since his illustrations of the clypeus show two distinct tubercles on the basal process. These specimens are most probably *B. wolfi*.

The penes of B. karroensis have been illustrated in the everted position. The apical part does appear shorter than in other species and it is possible that it is not fully everted. However, with the limited number of specimens available, the structure cannot be verified.

Branchipodopsis natalensis Barnard, 1929 Figs 23-24

Branchipodopsis natalensis Barnard, 1929: 196, fig. 50.

Material

Syntypes. NM 1384, $1 \circ (5 \text{ mm})$, $2 \circ (\text{no measurements})$; collected from Natal, half mile from Van Reenen (border of Orange Free State and Natal) (Barnard 1929). These specimens, apparently housed in the Natal Museum, Pietermaritzburg, could not be found in the institute's collections.

Material examined. SAM-40846, 10 δ (12.5 \pm 0.8 mm), 1 \Im (12.3 mm); collected from a small depression in a boulder, Bushman's Nek-Sehlabatebe Game Reserve area, Drakensberg, Natal, by M. Hamer and O. Wirminghaus, 23 April 1993. SAM-A40847, 4 δ (9.4-9.8 mm); collected from a small rock pool, Sehlabatebe Game Reserve area, Drakensberg, Lesotho, by M. Hamer and O. Wirminghaus, 24 April 1993. DB 818, 3 δ (9.3, 10.8, 11.4 mm), 2 \Im (both 12.3 mm); collected from Sehlabatebe Game Reserve, Lesotho, by T. Rutherford, 1985.

Redescription of adult male

Clypeus. Basal process apically bilobed with the inner lobe narrow and with a minute apical projection. Outer lobe rounded. Conical tubercle present on dorsal surface near base of inner lobe (Figs 23A, 24A-B). Lamelliform process small and oval. Apical joint curved inwards and with rounded apex. Median ventral process narrow and ovate.

Cercopods. Moderate length (approximate ratio to body length 0.2:1). Outer margins convex with plumose setae along entire length. Inner margins with sparse setae along proximal two-thirds; these replaced by 4–5 short spines on distal third (Fig. 23B).

Abdominal spines. Ventral surface of last abdominal segment with pair of small spines (Fig. 23C).

Penes. Proximal region of median margin with small, angular projection (Fig. 23D).



Fig. 23. Branchipodopsis natalensis (SAM-A40847). A. Dorsal view of clypeus; arrow indicates small projection on inner lobe. B. Cercopods of male. C. Ventral view of last abdominal segments of male; arrow indicates small spinous process. D. Ventral view of male genital segments showing basal part of penes; arrow indicates median rounded projection. E. Dorsal view of genital segments of female showing lateral extensions of last thoracic segment (indicated by arrow). F. Female second antenna. Scales = 0.5 mm.



Fig. 24. Branchipodopsis natalensis (SAM-A40847). A. Dorsal view of left half of clypeus. B. Detail of apical region of left basal process. Scales: A = 0.5 mm; $B = 100 \mu$ m.

Description of female

Thoracic segments. Last thoracic segment with slightly laterally and posteriorly extended surface (Fig. 23E).

Remarks

It is impossible to confirm the identification of the Sehlabatebe material without the type specimens of B. *natalensis*. However, since both sets of specimens come from high-altitude pools and there is a resemblance between the new material and Barnard's (1929) illustration and description of B. *natalensis*, it is possible that a single species is represented.

Some of the specimens had distinctly rounded apices of the apical joints, with the anteroventral surface expanded into a peg-like projection. There is, however, some intraspecific variation in this character and, since it was not described by Barnard (1929), it has been excluded from the above species description.

The cladistic analyses group B. natalensis with B. dayae, B. karroensis and B. hutchinsoni (Fig. 41). These species all share the bilobed basal process, with a small projection on the inner margin near the apex.

Branchipodopsis scambus Barnard, 1929 Figs 25-26

Branchipodopsis scambus Barnard, 1929: 199, fig. 5p.



Fig. 25. Branchipodopsis scambus. A. Dorsal view of clypeus (BMNH 1972.1.27.31-33).
B. Cercopods of male (AM LEN 18). C. Ventral view of basal part of penes (AM LEN 18); arrow indicates small rounded median projection. Scale = 0.5 mm.

Material

Type material. Barnard (1929) stated that the type specimens were collected in the Cape, Grahamstown, and were deposited in the Albany Museum. These have not been located.

Material examined. BMNH 1972.1.27.31-33, 1 \circ (12.8 mm), 1 \circ (15.2 mm); locality and date unknown, collected by K. G. McKenzie. AM LEN 18, 2 \circ (10.2, 11.8 mm), 1 \circ (15.0 mm); collected from flat, flooded grassland along Grahamstown-Cradock road, by F. de Moor, K. Martens and H. Barber, 28 November 1989. AM LEN 19, 1 \circ (10.1 mm), same collection data as AM LEN 18.

Redescription of adult male

Clypeus. Basal process slender, spiniform and apically acute (Figs 25A, 26A-B). Lamelliform process large and bluntly oval (Figs 25A, 26A). Apical

joint weakly curved, slender and smooth with rounded apex (Fig. 25A). Median ventral process oval and with longer spines apically (Fig. 25A).

Cercopods. Short (ratio to body length approximately 0.11:1), straight and with plumose setae along entire length of both inner and outer margins, excluding distal quarter of inner margins which have four spines and apices which have two spines (Fig. 25B).

Abdominal spines. Pair of spines on ventral surface of last abdominal segment.

Penes. Basal part short and with small projection halfway along median margin (Fig. 25C).

Remarks

Barnard (1929) made no comment on the cercopods of *B. scambus*. In the specimens examined, these are unusual for the genus in terms of length and the small number of spines on the inner margins. These features, together with the simple shape of the basal processes, could indicate that this species is a primitive form of *Branchipodopsis* (Fig. 41).

Distribution

The species is known only from the type locality of Grahamstown and the additional locality along the Grahamstown-Cradock road in the eastern Cape (Fig. 38).



Fig. 26. Branchipodopsis scambus (AM LEN 18). A. Dorsal view of clypeus. B. Detail of left basal process. Scales: A = 0.5 mm; $B = 100 \mu$ m.

Branchipodopsis simplex Barnard, 1924 Fig. 27

Branchipodopsis simplex Barnard, 1924: 217, pl. 26 (figs 2-3); 1929: 196, fig. 5b-c.

Material

Syntypes. SAM-A6006, 3 & (7.0, 8.0, 8.1 mm); collected from Eunda (about 100 miles west-north-west Ondangua), Ovamboland, Namibia, by K. H. Barnard, date unknown.

Other material examined. BMNH 1932.2.25.11-15, 1 ♂ (7.0 mm), 1 ♀ (8.3 mm); collected from Ovamboland, Namibia, collector and date unknown.

Redescription of adult male

Clypeus. Basal process with inflated proximal region, apically narrower and rounded (Fig. 27A). Dorsal keel present along length of basal process



Fig. 27. Branchipodopsis simplex (SAM-A6006, syntype). A. Dorsal view of clypeus; large arrow indicates dorsal keel; small arrow indicates apex of keel.
B. Lateral view of clypeus; arrow indicates keel. C. Cercopods of male. D. Ventral view of basal part of left penis. Scale = 0.5 mm.

(Fig. 27B). Lamelliform process small and rounded (Fig. 27A). Apical joint with distinct bend, distal to which posterior margin inflated. Apex of apical joint blunt (Fig. 27A). Median ventral process absent.

Cercopods. Moderate length (ratio to body length approximately 0.25 : 1) with outer margins weakly convex (Fig. 27C). Short setae on proximal part of inner margins and along length of outer margins. Distal two-thirds of inner margins with approximately 10 evenly spaced spines (Fig. 27C).

Abdominal spines. Spines on ventral surface of last segment absent.

Penes. Proximal region of basal part with median margin bulbous and with rounded projection about halfway along length (Fig. 27D).

Remarks

The keel of the basal processes is difficult to see, particularly in such small specimens, and is only obvious in lateral view (Fig. 27B). This character is autapomorphic, but *B. simplex* was consistently grouped with *B. kalaharensis* in the cladistic analyses (Fig. 41), even though the two species do not share many basal process features.

Distribution

Branchipodopsis simplex has only been collected from the type locality in Namibia (Fig. 38).

Branchipodopsis tridens Daday, 1910 Figs 28-31

Branchipodopsis tridens Daday, 1910: 308, fig. 53. Barnard, 1924: 217; 1929: 197, fig. 5d; 1935: 487. Linder, 1941: 228, fig. 30b.

Material

Type material. Consists of two male and two female specimens and is housed in the Senckenberg Museum; collected from the Kalahari, by D. Schultze, date unknown (Daday 1910).

Material examined. SAM-A5980, 1 δ (12.1 mm), 1 \circ (11.8 mm); collected from Papkuil, near Kimberley, Cape Province, by Miss Wilman, date unknown. SAM-A7255, 1 δ with cercopods missing; collected from Bak River, Cape Province, by K. H. Barnard, 1925. SAM-A6290, 1 δ , poor condition; collected from between Keimoes and Upington, Cape Province, 1909, collector unknown. SAM-A7257, specimens dehydrated; collected from Outjo, Kaokoveld, Namibia, by K. H. Barnard, 1926. SAM-A7256, specimens in poor condition; collected from Narugas siding, Cape Province, by K. H. Barnard, 1925. SAM-A7258, 2 δ in poor condition; collected from Kamanyab, Kaokoveld, Namibia, by K. H. Barnard, 1926. SAM-A7267, 3 δ (12.5, 12.6 mm; 1 with cercopods broken), 5 \circ (10.4-12.3 mm); collected from Cauas Okawa, Kaokoveld, Namibia, by K. H. Barnard, March 1926. SAM-A5922, 1 δ (19.0 mm); collected from Great Fish River, near Gibeon, Namibia, by R. W. Tucker, January 1916. SAM-A7599, 1 δ (cercopods removed), 12 \circ (poor condition); collected from Amadap Valley, Little Namagualand, Cape Province, by Dendy, 1938. SMN 51291, 8 & (6.5-7.9 mm), 10 9 (5.4-7.4 mm); collected from small pool in a rock kaross, Etosha Park, Namibia, by E. Griffen, 7 October 1986. SMN 51197, large number of specimens, 25 σ measured (9.0 + 0.6 mm), 22 φ measured (8.3 + 0.6 mm); collected from large shallow rock pool at the base of a rock hill (Bakenkop), Namib Naukluft Park, Namibia, by B. D. Collahan, 17 March 1986. SMN 51334, 1 & with broken abdomen; collected from Charl Marais Dam (Sukses Dam), Etosha Park, Namibia, by M. & P. Lindeque, 26 January 1988. TM VLKE443, large number of specimens, 33 & measured $(10.6 \pm 1.2 \text{ mm})$, 25 \circ measured $(10.8 \pm 1.2 \text{ mm})$; collected from Gori Pan (possibly Goru, Kangara), Botswana, by the VLKE, 20 April 1930. HNHM I/A-78, 3 & (9.1, 9.2, 10.2 mm), 2 9 (8.7, 10.2 mm); collected from Kalahari, Botswana, collector and date unknown. AM LEN 150A, large number of specimens, many immature, 14 \diamond measured (9.8 + 3.0 mm), 20 \circ measured $(8.8 \pm 0.8 \text{ mm})$; collected from Leeubron, Etosha Park, Namibia, by A. Bowland, November 1985. AM LEN 156A, 1 & (11.5 mm); hatched from sediment (5 February 1993) collected from rock pool on top of Moonrock, Augrabies Falls National Park, Cape Province, by M. Hamer, 19 December 1992. AM LEN 163A, 6 & (8.1-11.8 mm), 2 9 (9.3, 10.9 mm); hatched from sedi-ment (2 April 1993) collected from dry pool, 40 km south of Kalahari Gemsbok Park, Cape Province, by M. Hamer, 24 December 1992. SAM-A40850, 7 & (10.6-14.4 mm); hatched from sediment collected from granite rock cavity, 10 km north-east of Gobabeb, Kuiseb River bed, by J. A. Day, 24 June 1981. SAM-A40851, 2 & (15.6, 16.3 mm); hatched from sediment collected from Amichab, 140 km west of Rheboth, Namibia, by J. A. Day, 5 July 1981. SAM-A40852, 1 & (14.0 mm); locality data as for SAM- A40851; hatched from sediment collected by J. A. Day, 24 June 1981. DB 765, 1 3, 1 9 (both poor condition); collected from series of pools at Blutkoppie on granite outcrop, Namib Desert, Namibia, by J. A. Day, 27 March 1982. DB 767, 1 & (18.8 mm), 5 9 (10.9-13.8 mm); hatched from sediment collected from Gemsbokwater, 18 km north of Ganab, Namib Desert, Namibia, by J. A. Day, 14 May 1980. DB 768, $1 \, \delta$, $1 \, \varphi$ (both poor condition); hatched from sediment collected from 4 km north-north-west of Zebra Pan, Namib Naukluft Park, Namib Desert, Namibia, by J. A. Day, 2-12 May 1980.

Branchipodopsis cf. tridens, Namibia. DB 761, 2 \diamond (12.1, 12.5 mm); hatched from sediment collected from large gravel pool in desert plain near Heinrichsberg, Namib Desert, Namibia, by J. A. Day, 5 July 1981. DB 763, 4 \diamond (10.0-11.0 mm); collected from Mirabib, 2 sinkholes in granite inselberg, Namib Desert, Namibia, by J. A. Day, 26 March 1982. DB 764, 9 \diamond (13.1-15.8 mm), 25 \diamond (12.6 \pm 0.8 mm); hatched from sediment collected from Gemsbokwater, series of pools in granite desert floor, Namib Desert, Namibia, by J. A. Day, April 1978.

Branchipodopsis cf. tridens, Northern Transvaal and Zimbabwe. AM LEN 151A, 4δ (2 poor condition; others 6.9, 7.9 mm); collected from pool on rocky outcrop near Umzingwani River, Benfer Estates, Zimbabwe, by O. Wirminghaus, 8 July 1988. AM LEN 134B, 1δ (13.4 mm), $1 \Leftrightarrow$ (12.3 mm); collected from Mopane, 35 km south of Beit Bridge, Transvaal, by O. Wirminghaus, 31 December 1992.



Fig. 28. Branchipodopsis tridens. A. Dorsal view of clypeus, Etosha Park (SMN 51334).
B. Cercopods of male (SAM-A7267). C. Ventral view of last abdominal segments of male (SAM-A5980); arrow indicates spinous projection. D. Basal part of penes (SAM-A5980); arrow indicates median rounded projection. E-G. Variation in basal processes shown in dorsal view. E. Kalahari (HNHM I/A-78). F. Papkuil (SAM-A5980). G. Amadap Valley, Kalahari (SAM-A7599). H. Dorsal view of clypeus of HNHM I/A-78, showing shape of basal processes of larger specimen. Scales = 0.5 mm.



Fig. 29. A, C. Branchipodopsis tridens (AM LEN 163A, outside Kalahari Gemsbok Park).
A. Dorsal view of left half of clypeus. C. Detail of left basal process. B, D. Branchipodopsis cf. tridens (DB 764, Gemsbokwater). B. Dorsal view of left half of clypeus; white arrow indicates indentation in median margin; black arrow indicates projection on apical joint. D. Detail of left basal process. Scales: A-B = 0.5 mm; C-D = 100 μm.

Redescription of adult male

Clypeus. Basal process broad, distally with a large, angular inner lobe and a short, conical outer lobe. Inner lobe usually apically flat or slightly convexly rounded (Figs 28A, 29A-D) and with scale-like patterning on apex (Fig. 30A-C). Median margin of basal process usually with a distinct

indentation at base of inner lobe (Fig. 29A-D). Large conical/digitiform projection present proximally on dorsal surface of each basal process (Figs 28A, 29A-D). Lamelliform process narrow and ovate (Fig. 29A-D). Apical joint with distinct bend, and strongly curved inwards, usually apically indented or bifid (Fig. 28A). Median ventral process small and minutely setulose but in most cases absent.

Cercopods. Moderate length (ratio to body length approximately 0.25:1). Outer margins convex with short, plumose setae along three-quarters of length, distal quarter with 4–6 spines. Proximal third of inner margins with sparse, moderate length setae, followed by 12–16 sharp spines (Fig. 28B).

Abdominal spines. Pair of spines on last abdominal segment usually prominent (Fig. 28C).

Penes. Basal part broad, with distinct rounded projection proximally on median margin (Fig. 28D).

Remarks

A large amount of variation is evident in the clypeus of B. tridens from different localities. In some cases the variation may be attributed to the specimens not being fully mature or a result of poorly preserved material. The HNHM specimens are, presumably, part of the type material. The clypeus of even these three specimens shows variability in terms of the median margin indentation, shape of the inner lobe (Fig. 28E, H) and apex of the apical joint, and this is probably size related. Most of the specimens from the other localities are, however, fully developed and in fair condition but they still exhibit a certain amount of interpopulation variation in the shape of the lobes of the basal process, their relative lengths, the proportion of the dorsal, conical projection to that of the basal process and in the shape of the apex of the apical joint. The indentation in the median margin of the basal process is also variable in extent. In some specimens it is so pronounced as to form a narrow third lobe, whereas other specimens have a completely straight median margin. There are a number of sets of specimens with the median margin in a state intermediate between these two extremes. An attempt to divide the large number of specimens into morphological groups, based mainly on proportions of inner and outer lobes and dorsal process, failed because of a large amount of overlap of characters. Further comment on this intraspecific variation is made in the discussion section.

Certain of the Namib Desert specimens (DB 761, 762, 763, 764) do, however, have characters that allow them to be distinguished from the other *B. tridens* material. These specimens have a distinct, short and broad spinous projection just proximal to the bend in the apical joint (Figs 29B, 30D). This structure is absent in all other *B. tridens* specimens examined and from both Daday (1910) and Barnard's (1929) descriptions and illustrations. In addition, these specimens have a deep indentation in the median margin of the basal process, such that a narrow third lobe is formed (Fig. 32B, D), and the dorsal projection is broad and blunt as opposed to the conical and apically narrow process of other specimens. These differences could indicate that this material represents a species or population intermediate between *B. tridens* and *B. kaokoensis*.



Fig. 30. Branchipodopsis tridens. A. Detail of apex of inner lobe of left basal process (Namib Naukluft, SMN 51197). B. Detail of apex of inner lobe of right basal process (AM LEN 163A). C. Detail of apex of inner lobe, left basal process of Goru Pan specimen (TM VLKE443). D. Projection on apical joint of Gemsbokwater specimen (DB 764). Scales = 50 μm.

The Zimbabwe and Mopane specimens show the greatest difference from Daday's (1910) figures and specimens, and are easily distinguished from the remainder of the *B. tridens* material. The inner lobe is broadly hook-shaped with a convex median margin and the apex of the apical joint is tapered and narrow (Fig. 31A-B). For this reason, and because identical specimens have been collected from two localities, it is quite possible that they represent a closely related, but separate species from *B. tridens*. However, no material has been collected from the area between Namibia and northern Transvaal-southern Zimbabwe and the possibility of intermediate forms exists.



Fig. 31. Branchipodopsis cf. tridens (AM LEN 151A). A. Dorsal view of left half of clypeus, Zimbabwe specimens. B. Detail of basal processes. Scales = $100 \ \mu m$.

Until such time as collecting over greater areas of southern Africa has been done and further research into sexual isolation and molecular biology has been undertaken, it seems prudent to simply describe the variation observed without drawing any conclusions.

Distribution

Branchipodopsis tridens is widely distributed in the arid western region of southern Africa. A large number of records from northern Namibia exist, and this species has also been collected from the southern part of that country as well as the north-western Cape (Fig. 39). The Zimbabwe specimens represent the most easterly record of the species and *B. tridens* has also been collected from Bloemfontein in the central region of South Africa (Seaman et al. 1991).

Branchipodopsis underbergensis sp. nov. Figs 32-33

Material

Holotype. SAM-A40837, 1 \circ (14.4 mm); collected from rock pool on Bamboo Mountain, near Underberg, Drakensberg, Natal, by T. Clarke & N. Crouch, December 1993.

Paratypes. SAM-A40838, 15 \circ (14.3 \pm 0.6 mm), 8 \circ (12.0-15.0 mm); same collection data as holotype.

Other material examined. SAM-A40848, 24 \circ (10.7 \pm 0.6 mm), 29 \circ (10.1 \pm 0.7 mm); collected from Underberg, Drakensberg, Natal, collector and date unknown (specimens were previously in the teaching collection of the Zoology Department, University of Natal, Pietermaritzburg).

Description of male

Clypeus. Basal process positioned low on basal joint (apex not reaching past anterior median margin of basal joints) on inflated base, slender and digitiform (Figs 32A, 33A-B). Prominent short and conical projection on proximal, dorsal surface of basal process (Figs 32A-B, 33A-B). Apical region of basal process and projection patterned by series of rounded ridges and depressions (Fig. 33C). Median ventral process ovate and spinous with blunt apex (Figs 32A, 33A). Lamelliform process very large and round-ovate (Figs 32A, 33A). Apical joint curved inwards and with inflated apex (Figs 32A, 33A).

Cercopods. Long (ratio to body length approximately 0.35:1). Outer margins proximally convex, distal halves slightly concave and with short, spinous setae along entire length. Small patch of setae proximally on inner margins followed by about 14 short spines (Fig. 32C).

Abdominal spines. Pair of small spines on ventral surface of last abdominal segment (Fig. 32D).

Penes. Basal part short, with moderate-sized, rounded projection on median margin (Fig. 32E).

Description of female

Pair of small pouches on dorsal surface of penultimate thoracic segment and lateral surfaces of last thoracic segment extended outwards (Fig. 32F).

Egg morphology

Egg surface with irregular, four- to five-sided depressions, separated by narrow, sharp ridges (Fig. 33D).

Differential diagnosis

Superficially, *B. underbergensis* resembles *B. drakensbergensis*. This is largely because of the proximal projection of the basal process and the slender shape of the basal process. However, the fact that the basal process of the former species is single as opposed to bilobed in the latter, suggests two distinct species. Further differences include the very large lamelliform process in *B. underbergensis* and the small basal process positioned low on the basal segment of the clypeus of this species. The median ventral process also differs in shape, as do the cercopods. In addition, the females of *B. drakensbergensis* lack the thoracic pouches (Fig. 10F) that are distinct in *B. underbergensis* females.

Distribution

Branchipodopsis underbergensis has only been collected from the Underberg area of the Natal Drakensberg (Fig. 38).

Remarks

In spite of the general similarity between the basal processes of *B. drakens*bergensis and *B. underbergensis*, these two species were not linked in the cladistic analyses (Fig. 41). *Branchipodopsis underbergensis* was more frequently grouped close to *B. hodgsoni*. This may be possible since the dorsal



Fig. 32. Branchipodopsis underbergensis sp. nov. (SAM-A40838, paratype). A. Dorsal view of clypeus. B. Lateral view of clypeus; e-eye; s-spinous projection of basal process; lp-lamelliform process; l-labrum. C. Cercopods of male. D. Ventral view of last abdominal segments of male; arrow indicates spinous projection. E. Ventral view of basal part of penes. F. Dorsal view of genital segments of female; small arrow indicates dorsal extensions; large arrow indicates posterior lateral extensions. Scales = 0.5 mm.

process on the basal process of *B. underbergensis* could be homologous to the dorsal lobe of the basal process of *B. hodgsoni* rather than the spinous process in *B. tridens*, *B. kaokoensis* and *B. drakensbergensis*. The low position of the basal process in *B. underbergensis* and in *B. hodgsoni* could provide further evidence for the relationship between these two species.



Fig. 33. Branchipodopsis underbergensis sp. nov. (SAM-A40838, paratype). A. Dorsal view of left part of clypeus. B. Detail of left basal process, arrow indicates spinous projection. C. Detail of apical region of basal process lobe. D. Egg. Scales: A = 0.5 mm; B, $D = 100 \ \mu\text{m}$; $C = 10 \ \mu\text{m}$.

Etymology

Branchipodopsis underbergensis is named after the type locality, Underberg.

Branchipodopsis wolfi Daday, 1910 Figs 34-37

Branchipodopsis wolfi Daday, 1910: 304, fig. 52; 1913: 4. Barnard, 1924: 217; 1929: 197, fig. 5g.

Material

Type material. Collected in the Kalahari and housed in the Senckenberg Museum. No further information available.

Material examined. SAM-A7268, 1 & (11.9 mm), 1 9 (10.3 mm); collected from Altmark, Outjo district, Namibia, by K. H. Barnard, January 1926. SAM-A6004, 18 3 (6.5 \pm 0.5 mm), 15 9 (6.5 \pm 0.4 mm); collected from Onganjera, Ovamboland, Namibia, by K. H. Barnard, 1926. SAM-A5920, 5 & (11.9-15.6 mm); collected from Beaufort West, Karoo, Cape Province, by W. F. Purcell, 24 September 1905. SAM-A7253, 20 & (6.3 ± 0.6 mm), 11 ° (5.8 ± 0.5 mm); collected from Kamanyab, Kaokoveld, Namibia, by K. H. Barnard, 1926. SAM-A7273, 8 3 (10.0-12.0 mm), 9 9 (10.0-11.5 mm); collected southeast of Choabendus, Kaokoveld, Namibia, by K. H. Barnard, January 1926. SAM-A5921, 19 \circ (12.8 \pm 1.5 mm), 13 \circ (12.1 \pm 0.9 mm); collected from Great Fish River, near Gibeon, Namibia, by R. W. Tucker, January 1916. SAM-A4248, large number of specimens, 23 σ measured (7.8 \pm 0.8 mm), 15 \circ measured (7.9 \pm 0.8 mm); collected from Kimberley, Cape Province, by J. H. Power, 1917. SAM-A7254, 9 & (12.8-14.8 mm), 1 9 (15.0 mm); collected from Kimberley, Cape Province, by J. H. Powers, 1917. SAM-A6005. 5 \circ (8.5–10.5 mm), 21 \circ (8.6 \pm 0.7 mm); collected from Waterberg, Namibia, by R. W. Tucker, 1920. SMN 51217, 5 ♂ (8.0–9.1 mm), 6 ♀ (7.8–8.8 mm); collected from rain pool near Otjituuo, Hereroland West, Namibia, by B. A. Curtis, 28 April 1987. HNHM I/A-77, 1 & (8.9 mm), 1 9 (8.2 mm); collected from Kalahari, Botswana, collector and date unknown. AM LEN 99B, 4 3 (14.8-15.3 mm), 8 9 (9.5-11.3 mm); collected from Pumbe Pan, Kruger National Park, Transvaal, by M. Hamer, 28 October 1990. AM LEN 154A, 3 d (8.1, 9.6, 10.0 mm), 5 9 (8.9-9.5 mm); collected from Nylsvlei Nature Reserve, Transvaal, by C. Pitzke-Widdig & T. Widdig, February 1990. DB 668, 1 & (12.5 mm), 5 9 (10.0-13.0 mm); collected from Machoarane Mountain, about 2 km south of Morija (Moraija), Lesotho, by T. C. Rutherford, 8 November 1985. DB 667, 1 \Im (abdomen removed), 2 \Im (10.1, 12.8 mm); collected from Brakfontein, 17 km south of Mohales Hoek, Lesotho, by T. C. Rutherford, 12 December 1985. DB 669, 8 & (8.1-13.9 mm), 7 9 (11.3-12.8 mm); collected from Leloaleng near Quting, Lesotho, by T. C. Rutherford, 13 December 1985. DB 817, 3 & (14.0, 16.4, 17.0 mm), 3 9 (13.0, 13.9, 15.6 mm); collected from Outward Bound, Leribe, Lesotho, by T. C. Rutherford, 4 January 1986.

Branchipodopsis cf. wolfi, Transvaal. AM LEN 69B, 3 \circ (8.5, 8.8, 9.0 mm), 2 \circ (8.0, 9.8 mm); collected from Mala Mala Game Reserve, Transvaal, by W. A. Taylor, 25 June 1989. AM LEN 155A, 3 \circ (9.9, 11.1, 11.3 mm); cultured from dried sediment (February 1990) collected from Mala Mala Game Reserve, Kirkmans Kamp area, Transvaal, by M. Hamer, September 1989. AM LEN 120A, 7 \circ (7.8–10.0 mm), 2 \circ (6.8, 9.5 mm); collected from region south of Skukuza, Kruger National Park, Transvaal, by A. & J. Bowland, 14 October 1990. AM LEN 121B, 15 \circ (9.8 \pm 0.6 mm), 22 \circ (8.7 \pm 0.5 mm); same collection data as AM LEN 120A.

Branchipodopsis cf. wolfi, Zimbabwe. NMZ/Cr 29, 1 ♂ (damaged), 3 ♀ (damaged); collected from Matopos, Zimbabwe, December 1964, collector

unknown. NMZ/Cr 6, 9 δ (15.0-20.6 mm), 14 \circ (17.9 \pm 2.0 mm); collected from Matopos, Zimbabwe, by A. N. Smith, December 1981. USNM 184629, 3 δ (9.0, 9.3, 9.4 mm), 2 \circ (8.1, 8.6 mm); collected from Bulawayo, Zimbabwe, by D. H. Eccles & W. G. Moore, 10 February 1955. USNM 102318, 3 δ (8.8, 9.0, 10.6 mm), 1 \circ (9.5 mm); collected from pools at isoyds of the tomb of Cecil John Rhodes, 25 miles south-south-west of Bulawayo, Zimbabwe, by D. H. Eccles, 10 February 1955.

Redescription of adult male

Clypeus. Basal process wide with single large, conical or triangular lobe positioned on inner side of basal process and two apical tubercles (Figs 34A, 35A-D). Lateral tubercle digitiform/conical and positioned slightly ventrally (Fig. 36A-D). Median tubercle usually similar in size and shape to outer



Fig. 34. Branchipodopsis wolfi. A. Dorsal view of clypeus of specimen HNHM I/A-77 from Daday's collection. B. Cercopods of male (AM LEN 99B). C. Ventral view of last abdominal segments of male (AM LEN 99B) showing spinous processes (indicated by arrows). Di. Dorsal view of basal part of right penis (SAM-A5921); arrow indicates blunt projection. Dii. Ventral view of apex of basal part of right penis (SAM-A5921); arrow indicates blunt projection on lateral surface.

Scales =
$$0.5 \text{ mm}$$



Fig. 35. Branchipodopsis wolfi. A. Left half of clypeus, Lesotho specimen (DB 669).
B. Left half of clypeus of specimen from Pumbe, Kruger National Park (AM LEN 99B).
C. Left half of clypeus of Great Fish River specimen (SAM-A5921). D. Clypeus of Altmark specimen (SAM-A7268). Scales = 0.5 mm.

tubercle and situated dorsally at base of inner lobe (Figs 36A-D, 37B-C, F). A small, flattened projection often present on median apex of lobe (Figs 36A, C, 37D, F). Lamelliform process small and round or oval (Figs 34A, 35A-D). Apical joint curved inwards with apex varying from flattened (Fig. 35B) to slightly indented (Fig. 35D). Median ventral process very small to large and prominent, usually oval and with surface covered by short spines (Fig. 35A-D).



Fig. 36. Branchipodopsis wolfi. A. Detail of left basal process of DB 669 specimen; il—inner lobe; lt—lateral tubercle; mt—median tubercle; pr—projection on inner lobe. B. Detail of left basal process of AM LEN 99B. C. Detail of left basal process of SAM-A5921. D. Detail of right basal process of SAM-A7268 (arrow indicates lateral tubercle). Scales = $100 \,\mu$ m.

Cercopods. Average length (ratio to body length approximately 0.27:1). Outer margins weakly convex and with plumose setae of moderate length but these replaced by 2–4 short spines distally. Proximal third of inner margins with plumose setae followed by 10–16 spines of unequal size (Fig. 34B).

Abdominal spines. Last abdominal segment with two strong ventral spines (Fig. 34C).

Penes. Basal part slender, with proximal rounded projection on median margin. Peg-like projection near apex on lateral margin (Fig. 34D-E).

Remarks

Much variation is evident in the clypeus of B. wolfi from different localities. This was observed and commented on by Barnard (1929). Variation is most obvious in the following features of the clypeus: the apex of the apical joint, the



Fig. 37. Branchipodopsis cf. wolfi. A. Dorsal view of clypeus of southern Kruger National Park specimen (AM LEN 121B). B. Left basal process of AM LEN 121B. C. Right basal process of Mala Mala specimen (AM LEN 155A); outer tubercle indicated by arrow. D. Detail of apical region of basal process (AM LEN 121B); il—inner lobe; mt—median tubercle; pr—projection on inner lobe. E. Basal processes, Zimbabwe specimen (NMZ/Cr 6). F. Detail of apical region of right basal process of NMZ/Cr 6. Scales: A-B, E = 0.5 mm; C, F = 100 μ m; D = 50 μ m.

shape of the tubercles and the inner lobe, the presence and shape of a projection on the inner lobe, the relative lengths of the tubercles, the position and size of the median tubercle, and the shape of the median margin of the basal process.

The HNHM specimens are possibly the types, as they are from Daday's collection and from the same locality as the types. In these specimens, the tubercles and inner lobe are rather short and rounded and all of similar shape. A small apical projection is present on the inner lobe. The median margin has an inflation just proximal to the base of the inner lobe. Most of the other specimens show some variation on this basic arrangement. The median tubercle of the Lesotho specimens is small and lies in the same plane as the inner lobe and the apical process is very prominent and rounded (Fig. 36A). In the Altmark specimen, the inner lobe is roughly triangular and lacks the apical projection (Fig. 36D). The Kruger Park (Pumbe) specimens have an angular median margin and a very broad inner lobe (Fig. 36B). It is, however, the Zimbabwean and southern Kruger Park specimens that show the greatest morphological divergence from the 'types' of B. wolfi. The median tubercle is small and triangular and is situated about halfway along the length of the inner lobe (Fig. 37B, F). These Zimbabwean and southern Kruger Park specimens could be regarded as a separate species but have been included with B. wolfi because there is a series of specimens in which the basal process morphologies are intermediate between these and the other, more typical representatives. For example, the Mala Mala specimens have a larger median tubercle than the other two sets of specimens. those from the Kruger Park have a slightly smaller tubercle, and the Zimbabwe specimens have an even smaller one. These specimens, therefore, form a series from a prominent to a small median tubercle and yet all three sets share a very similar basal process shape. The specimens from Nylsvlei have a basal process morphology intermediate between the Kruger Park. Mala Mala and Zimbabwe specimens and other, more typical, B. wolfi specimens, and this makes it impossible to divide, with any confidence, these specimens into separate species or subspecies at this stage.

The structure of the basal process of B. wolfi can be interpreted in a number of different ways and this further complicates any attempt to identify species or subspecies, and to determine relationships with other species of the genus. It is uncertain whether the median tubercle illustrated in Figure 36B and D is homologous to that illustrated in Figures 36A and 37B and F. In addition, the inner lobe could be interpreted as a third tubercle and the lateral tubercle could represent a second lobe. The latter interpretation was included in one of the cladistic analyses but did not result in B. wolfi being grouped differently to those patterns illustrated in Figure 41.

Distribution

As Barnard (1929) stated, *B. wolfi* is the most widely distributed species of *Branchipodopsis*. This species occurs in arid northern and southern Namibia, the northern Cape and Karoo, in the sub-tropical eastern Transvaal and Zimbabwe, and in the high-altitude, mountainous habitats of eastern Lesotho (Fig. 40). *Branchipodopsis wolfi* was also collected from Umfolozi Game Reserve in north-eastern Natal, but these specimens had dried out and they were not listed under specimens examined. An additional set of specimens from pools

outside Gaberone was examined and identified as *B. wolfi* for Dr M. Cantrell, formerly of the University of Botswana. Barnard (1929) referred to the presence of *B. wolfi* in Kenya but illustrations or specimens from there have not been seen and so this locality cannot be verified. A set of specimens in the BMNH from '40 km north of Soroti in the eastern province of Uganda' were examined and their identification as *B. wolfi* confirmed in terms of the features of the species as presented here. This record may indicate a wider distribution of *B. wolfi* than for the other southern African *Branchipodopsis* species.

KEY TO THE SOUTHERN AFRICAN SPECIES OF THE GENUS *BRANCHIPODOPSIS* (using features of the male clypeus)

| 1A. 1B. | Basal process distinctly bilobed apically, lobes of similar height and positioned adjacent to each other |
|------------|---|
| | different heights or not positioned adjacent to each other |
| 2A. | Basal process with tubercle on median dorsal surface and smaller projec- tion on median margin of inner lobe |
| 2B. | Basal process with small projection on median surface of inner lobe only |
| 3A. | Basal process lobes equal in size and shape, apex of apical joint blunt, lamelliform processes broadly oval, with scalloped margin |
| 3B. | Inner lobe of basal process narrower than outer, apex of apical joint peg-like or rounded, lamelliform processes narrow oval with smooth margin |
| 4A. | Inner lobe of basal process more conical than rounded, lamelliform process small, distal region of apical joint foot-shaped |
| 4B. | Both lobes of basal process rounded, lamelliform process distinct, distal region of apical joint with slight inflation and with blunt tip |
| 5A. | Basal process with large, spine-like or conical projection proximally on dorsal surface |
| 5B. | Basal process without proximal spine-like or conical projection9 |
| 6A. | Basal process with three distinct lobes, inner and outer lobes similar in size and smaller than median lobe |
| 6B. | Basal process with only one or two distinct lobes |
| 7A. | Basal process with one or two lobes, narrower than high, median ventral process prominent |
| 7B. | Basal process wider than high, median ventral process vestigial or absent <i>B. tridens</i> Daday, 1910 (Figs 28-31) |

| 8A. | Basal process bilobed and almost as high as division between basal and apical joints, lamelliform process smaller than basal process |
|---------------|--|
| 8B. | Basal process with single lobe and lower than anterior median margin of basal joint, lamelliform process very large (larger than basal process) B. underbergensis sp. nov. (Figs 32-33) |
| 9A. 9B. | Basal process with single lobe, dorsal or apical tubercles or projections present |
| 10A. | Basal process with inflated base, rounded apex and with keel-like |
| 10B. | structure dorsally B. simplex Barnard, 1924 (Fig. 27) Basal process without keel-like structure dorsally, but with one or more tubercles or projections near apex |
| 11 A . | Basal process with two digitiform or conical tubercles apically, projecting beyond anterior margin of basal process, lamelliform processes small or moderate-sized |
| 11 B . | Basal process without apical tubercles projecting beyond anterior margin, lamelliform processes enlarged B. browni Barnard, 1924 (Figs 6-7) |
| 12A. | Two tubercles present, second positioned ventrally to first, distinct inner |
| 1 2B . | Two tubercles present, one median and one ventrolateral, large inner lobe present |
| 13A. | Basal process with single lobe of spiniform shape |
| 1 3B . | Basal process bilobed, outer lobe distinctly shorter than inner lobe 14 |
| 14A. | Width of basal process greater than or equal to height, apical joint stout and strongly inwardly curved with distinct bend |
| 1 4B . | Basal process longer than wide, apical joint slender, weakly curved and without distinct bend |
| 15A. | Apical joint distally hook-shaped, median ventral process present |
| 15 B . | Apical joint distally smooth and straight, median ventral process absent B. barnardi sp. nov. (Figs 4–5) |

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DISCUSSION

Of the approximately 21 known species of *Branchipodopsis*, 16, including the five new species described here, occur in southern Africa and 15 of these are apparently restricted to this region. There is little morphological variety among the three Asian *Branchipodopsis* species and it has even been suggested that they may belong to a single species (Hartland-Rowe 1968; Brtek *et al.* 1984). The status and morphology of the two remaining *Branchipodopsis* species, namely *B. abiadi* from Mauritania in West Africa and *B. candea* from central Africa, are uncertain since these specimens are unavailable, and either the descriptions are inadequate or, in the case of the latter species, the original description cannot be located.

Taxonomic characters

The second antennae of the male, as in most other anostracan genera, is the character of greatest taxonomic value within the genus *Branchipodopsis*. The male anostracans use the enlarged, two-jointed antennae to clasp the female during mating. Belk (1991) found that, within the Anostraca, mating depends on female choice, with males attempting to mate completely unselectively. The female does not, however, always successfully recognize conspecific males by the structure of the antenna or by body armature or cercopod structure. This statement was based on Wiman's (1979) findings that hybridization occurred between North American species of *Streptocephalus* both in the laboratory and, under sympatric conditions, in the field. Selection, therefore, is not for anti-hybridization mechanisms. Belk (1991) suggested that the second antennae,



Fig. 38. Map of southern Africa illustrating the distribution of Branchipodopsis browni (open circle), B. drepane (open star), B. hodgsoni (open square), B. kalaharensis (closed triangle), B. kaokoensis (closed square), B. karroensis (closed circle), B. natalensis (flower), B. simplex (open, inverted triangle) and B. scambus (closed star).



Fig. 39. Map of southern Africa illustrating the distribution of *Branchipodopsis tridens* (closed circle), *B. hutchinsoni* sp. nov. (closed star), *B. drakensbergensis* sp. nov. (open square) and *B. barnardi* (flower).

because of their function in mating, are ideal candidates for runaway sexual selection by female choice and their 'elaborate structure should be viewed as arbitrary additions to the complexity of structures providing tactile clues'. Speciation in anostracans appears to be the result of the slow accumulation of genetic differences in allopatric populations (Wiman 1979).

In contrast to the streptocephalids, in which the male cercopod setation, frontal appendage, abdominal armature and external egg morphology are frequently species-specific, these characters either vary little between species of *Branchipodopsis* or they are largely absent. Authors such as Linder (1941) emphasized the structure of the penes as taxonomic characters at the familial and generic levels, but between species these do not differ to any extent. There is some interspecific variation in the prominence of the rounded projection on the median margin of the penes in the *Branchipodopsis* species examined but this is difficult to quantify and is often dependent on the preservation method or condition of the specimens. The peg-like projection at the apex of the proximal part of the penes is very obvious in some species, whereas in others only a blunt obscure projection is present. In other species, no distal lateral projection of any kind is visible. In certain cases, preservation state is responsible for the variation but this structure is quite clearly absent in some species. Unfortunately, these structures do not appear to reflect relationships between species. Within Branchipodopsis there is little interspecific variation in cercopod shape or setation; the number of spines on the inner margin does vary to some extent between species but there is a significant amount of overlap and intraspecific variation. External egg morphology is also of limited value for the same reasons (pers. obs.). Body armature, such as that seen in certain Streptocephalus species, is absent in Branchipodopsis with the exception of the two spines on the ventral surface of the last abdominal segment. However, this character does not appear to reflect species relationships. It is often present in species with very different antennal morphologies and, since these spines are present in approximately half the described species, they cannot be used for species identification. A character not mentioned by other authors but used in this review is the presence, position and shape of pouches proximal to the genital segments of the females of some species. The significance of these structures is uncertain but, since they only occur in high-altitude species (B. barnardi, B. underbergensis and B. natalensis), they may be of physiological importance. Until proved otherwise, these structures provide a useful additional character in separating species with similar basal process morphologies, such as B. natalensis and B. hutchinsoni, and B. drakensbergensis and B. underbergensis.



Fig. 40. Map of southern Africa illustrating the distribution of *Branchipodopsis wolfi* (closed square), *B. underbergensis* sp. nov. (open triangle) and *B. dayae* sp. nov. (open circle).

Species groups and systematic analyses

An attempt was made to divide the southern African species of *Branchipod*opsis into species groups. This was recently done for the African streptocephalids (Hamer et al. 1994a, 1994b) as a step towards understanding relationships between species and in examining the biogeography of the genus Streptocephalus. For the southern African species of Branchipodopsis, a combination of cladograms was used to achieve this division. The cladistic analyses and the groupings resulting from them must be seen as tentative, since inadequate data are available on the morphology, ontogeny and evolution of the genus and family. For example, it is almost impossible to determine, with any degree of confidence, homologous structures, incidences of homoplasy or to be certain of the pleisiomorphic and apomorphic states. Outgroup selection is also problematic since the characters and members of the Branchipodidae require total revision. The limited number of characters (Table 1) and, in certain species, specimens, that can be used, is a further limitation to these analyses. The relatively low RI and CI indices obtained from the Hennig86 analyses indicates a large amount of homoplasy and a low confidence level in the trees produced. Changing the interpretation of some characters and excluding others did not improve these values nor did it produce groupings notably different from the two illustrated in Figure 41. This could indicate that the species groups have some credibility.

TABLE 1

Tentative ordering of the southern African *Branchipodopsis* into species groups based on cladistic and phenetic analyses.

| Group | Characters | Species |
|-------|--|--|
| 1 | Basal processes simple, spine-like, apical joint weakly curved. | B. scambus |
| 2 | Basal processes with dorsal and ventral lobe, and set low on basal joints | B. hodgsoni B. underbergensis |
| 3 | Basal processes with single lobe, small projection on median, apical margin, second projection/tubercle on dorsal median surface | B. browni B. wolfi |
| 4 | Basal processes with two lobes, almost equal in size, one or more projections on basal processes. | B. natalensis B. hutchinsoni B. karroensis B. dayae |
| 5 | Basal processes narrow, bilobed, with smaller outer lobe than inner | B. drepane B. barnardi |
| 6 | Basal processes broad, apical joints strongly bent, median ventral process absent | B. kalaharensis B. simplex |
| 7 | Basal processes with dorsal spinous projection, 2 or 3 unequal-sized lobes. | B. kaokoensis B. tridens B. drakensbergensis |



Fig. 41. Cladograms of the southern African species of the genus *Branchipodopsis*. A produced from the command 'mhennig', with length of 35, ci value of 42, and ri of 66. B produced by the command 'ie-', with length of 45, ci of 42 and ri of 62.

Intraspecific variation

The large amount of variation observed in the basal processes of B. wolfi and B. tridens presented a major problem in this study. Specimens of these two species from some localities differed considerably from the original description and the type material in terms of antennal and, particularly, basal process morphology. However, other sets of specimens had basal process morphologies intermediate between these and the original material. Attempts were made to group populations of B. tridens or B. wolfi with the most similar basal process structure morphometrically. However, these results indicated a large degree of overlap and no distinct clusters, which would have been the case if different species were involved. Thus, the variation was simply described and/or illustrated. In the case of B. wolfi, antennal variation was evident in almost every population and it was impossible to illustrate all of this. Similar intraspecific variation was also observed and illustrated in the Asian species B. affinis (Brtek et al. 1984). In the case of these three species, more advanced taxonomic methods, most important of which will certainly be molecular techniques, are necessary to determine the relevance of this variation. At this stage, however, lack of sufficient quantities of material of all representative populations presents the major obstruction to such a study.

Distribution and ecology

An in-depth discussion of the biogeography of Branchipodopsis will be published elsewhere and only a brief comment will be made here about distribution and habitats. The majority of Branchipodopsis specimens were collected from small waterbodies, such as roadside ditches, shallow rain pools and small rock pools, where conditions would be expected to be extreme. Observations under both laboratory and field conditions have revealed that a number of Branchipodopsis species (B. tridens, B. wolfi, B. dayae and B. browni) grow very rapidly and reach sexual maturity 4-6 days after hatching. Their life span is only 2-4 weeks. This contracted life history allows members of the genus to exploit habitats not available to the other main group of southern African anostracans, the streptocephalids, which generally have a slower, longer life history. Species of the genus Streptocephalus have never been collected from high-altitude rock pools, thus allowing Branchipodopsis to dominate such habitats. Belk (1991) found a similar situation with S. texanus and Branchinecta packardi in central Texas. In temporary pools in southern Africa where Streptocephalus occurs, Branchipodopsis species are either absent, or are found in low numbers and complete their life history before the streptocephalids reach maturity, or they occupy a different niche. This may imply a reduced competitive ability for the genus. Further evidence for this is the rarity of the presence of more than one species in a single habitat. Barnard (1929) reported that two male B. drepane were found among a sample of B. tridens and B. wolfi but this is the only known case of multispecies existence. This could be a result of the restricted resources in habitats such as montane rock pools; but the forces separating species such as B. barnardi and B. natalensis, which inhabit the same type of rock pools in the Drakensberg in an area of less than 5 km^2 , are not known. Perhaps, as has been suggested (Wiman 1979; Williams 1985;

Brendonck et al. 1990), branchiopods are adapted to resisting, rather than promoting, dispersal, which may be a rare occurrence.

Williams & Busby (1991) suggested that only in episodically filled temporary pools could one expect to find widespread and easily dispersed species. The reason for this is that the irregularity of filling of such habitats does not allow the evolution of local adaptations and subsequent speciation. Many *Branchipodopsis* habitats, however, because of their small size, are likely to undergo a number of wet and dry phases during a single rainy season. As a result, many *Branchipodopsis* generations could be expected to hatch, as opposed to a single generation in large pools that remain full for the duration of the rainy season, or those that only fill every decade or less often. This would allow relatively rapid differentiation and could account for the large amount of intraspecific variation in species such as *B. wolfi* and *B. tridens*.

Conclusions

Southern Africa has the greatest diversity of species of *Branchipodopsis*. As suggested by Banarescu (1990), this may be as a result of the genus having a Gondwanaland origin, or the result of a wide adaptive radiation having occurred in response to the habitat diversity present in southern Africa. However, of the 16 species now described, four species (B. drepane, B. kaokoensis, B. karroensis and B. simplex) are known only from a single collection (the type material) consisting of fewer than 5 male specimens. For an additional species (B. hutchinsoni), only the type material has been collected, although this is in larger quantities than for the former species. Most species appear to have restricted distributions and it is possible that some of the species that were last collected early this century have become extinct. Further collecting will certainly reveal a number of undescribed species, as will research into intraspecific variation using molecular techniques to examine mitochondrial DNA. The distribution of species also needs to be reassessed as previously unexplored areas, such as the northern and western Transvaal, Zimbabwe, Botswana and Mozambique, are sampled. Detailed investigation of species relationships and of the position of the genus within the Branchipodidae needs to be undertaken to answer the taxonomic questions raised here.

ACKNOWLEDGEMENTS

The senior author was in receipt of a Foundation for Research Development (FRD) bursary. The directors and curators of the museums from which material was loaned, in particular Dr F. de Moor and Mrs H. James of the AM, Mrs M. van der Merwe of the SAM, Ms B. Curtis of the SMN, Dr L. Forró of the HNHM, Ms S. Halsey and Dr G. Boxshall of the BMNH and Dr T. Bowman of the USNM, are thanked for their co-operation. Dr J. A. Day of the University of Cape Town, and Dr D. Belk of Our Lady of the Lake University, San Antonio, provided material collected in Namibia, the Cape and Lesotho. The National and Natal Parks Boards gave permission to collect in areas under their control and field staff gave necessary advice and assistance on a number of occasions. The staff of the Electron Microscope Unit of the University of Natal,

Pietermaritzburg, are thanked for their assistance with electron microscopy, particularly Mrs P. Donnelly who printed the micrographs. Dr J. Brtek kindly provided valuable literature, references and a species list. Prof. G. Mura and Drs D. Belk and B. Cook made valuable comments on the manuscript. Mr O. Wirminghaus, Dr N. Rayner and Mr R. Struckmeyer are thanked for various forms of assistance rendered during this study.

REFERENCES

- BAIRD, W. 1852. Monograph of the family Branchipodidae, a family of crustaceans belonging to the division Entomostraca, with a description of a new genus and species of the family, and two new species belonging to the family Limnadiadidae. *Proceedings of* the Zoological Society of London 20: 18-37.
- BANARESCU, P. 1990. Zoogeography of fresh waters. General distribution and dispersal of freshwater animals 1. Wiesbaden: Aula-Verlag.
- BARNARD, K. H. 1924. Contributions to a knowledge of the fauna of South-West Africa. 2. Crustacea, Entomostraca, Phyllopoda. Annals of the South African Museum 20: 213-228.
- BARNARD, K. H. 1929. Contributions to the fauna of South Africa. A revision of South African Branchiopoda (Phyllopoda). Annals of the South African Museum 29: 181-272.
- BARNARD, K. H. 1935. Scientific results of the Vernay-Lang Kalahari Expedition, March-September, 1930. Crustacea. Annals of the Transvaal Museum 16: 481-492.
- BATTISH, S. K. 1983. On the occurrence of three species of fairy-shrimps: Anostraca: Crustacea in Punjab, with a checklist of Indian anostracans. *Researches on Crustacea* 12: 77-84.
- BELK, D. 1991. Anostracan mating behaviour: a case of scramble competition polygyny. In: BAUER, R. T. & MARTIN, J. W. eds. Crustacean sexual biology: 111-125. New York: Columbia University Press.
- BRAUER, F. 1877. Beiträge zur kenntnis der Phyllopoden. Sitzungsberichte der K. Akademie der Wissenschaften, Wien 75: 583-614.
- BREHM, V. 1958. Crustacea: Phyllopoda und Copepoda Calanoida. In: HANSTRÖM, B., BRINCK, P. & RUDERBECK, G. eds. South African animal life 5: 10–39.
- BRENDONCK, L., THIERY, A. & COOMANS, A. 1990. Taxonomy and biogeography of the Galapagos branchiopod fauna (Anostraca, Notostraca, Spinicaudata). Journal of Crustacean Biology 10: 676-694.
- BRTEK, J. 1972. Tanymastigites cyrenaica n.g., n.sp. und Notizen zur Taxonomie der Familie Branchipodidae. Annotationes Zoologicae et Botanicae, Bratislava 80: 1-6.
- BRTEK, J., FORRÓ, L. & PONYI, J. E. 1984. Contributions to the knowledge of the Branchiopoda: Crustacea fauna of Mongolia. Annales historico-naturales Musei nationalis hungarici, Budapest 76: 91-99.
- DADAY, E. 1910. Monographie systématique des Phyllopodes Anostracés. Annales des sciences naturelles (4° série, Zoologie) 11: 91-489.
- DADAY, E. 1913. Phyllopoda In: Voyage de Ch. Alluaud et R. Jeannel en Afrique orientale, 1911-1912. Résultats scientifiques. Crustacés 1: 1-9. Paris: Schulz.
- *DYBOWSKI, B. 1927. Ueber eine mene Form von Branchipus, Mongolobranchipus talkobryncewiczi Dyb. nov. sp. aus der Umgegend von Troickosanskan den Nordgrenze der Mongolei. Bulletin international de l'Académie des sciences et des lettres de Cracovie (B, Sciences naturelles) 1927: 39-43.
- FORRÓ, L. & BRTEK, J. 1984. Anostraca and Conchostraca taxa described by E. Daday together with a catalogue of pertinent material in the Hungarian Natural History Museum. *Miscellanea Zoologica Hungarica* 2: 75-104.
- HAMER, M. & APPLETON, C. 1991. Physical and chemical characteristics and phyllopod fauna of temporary pools in north-eastern Natal, Republic of South Africa. *Hydrobiologia* 212: 95-104.
- HAMER, M., BRENDONCK, L., COOMANS, A. & APPLETON, C. 1994a. A review of African Streptocephalidae (Crustacea: Branchiopoda: Anostraca). Part 1. Africa south of the Zambezi and Kunene rivers. Archiv für Hydrobiologie Supplement 99 (3): 279-311.

- HAMER, M., BRENDONCK, L., APPLETON, C. & COOMANS, A. 1994b. A review of African Streptocephalidae (Crustacea: Branchiopoda: Anostraca). Part 2. Africa north of the Zambezi and Kunene rivers, and Madagascar. Archiv für Hydrobiologie Supplement 99 (3): 235-277.
- HARTLAND-ROWE, R. 1968. The genus Branchipodopsis in Asia (Anostraca). Crustaceana 15: 214-215.
- LINDER, F. 1941. Contributions to the morphology and the taxonomy of the Branchiopoda Anostraca. Zooligska bidrag från Uppsala 20: 101-302. *LOFFLER, H. 1968. Die Crustaceenfauna der binnengewasser ost-afrikanischer
- Hochgebirge. Hochgebirgsforschung 1: 107-170.
- MALHOTRA, Y. R. & DUDA, P. L. 1970. A new fairy shrimp, Branchinecta acanthopenes n.sp. (Anostraca, Branchinectidae) from India. Crustaceana 18: 173-176.
- MASI, L. 1925. Descrizione di due Fillopodi anostraci della Somalia Italiana, Annali del Museo civico di storia naturale Giacomo Doria 52: 93-99.
- PESTA, O. 1921. Kritische revision der Branchipodidensammlung des Wiener naturhistorischen Staatsmuseums. Annalen des Naturhistorischen Museums in Wien 34: 80-98.
- *ROEN, U. 1952. On some Euphyllopoda from North China. Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kjøbenhavn 114: 203-215.
- SARS, G. O. 1898. On some South African Phyllopoda raised from dried mud. Archiv for Mathematik og Naturvidenskab 20 (4): 1-43.
- SARS, G. O. 1901. On the Crustacean fauna of Central Asia. Part 1: Amphipoda and Phyllopoda. Annuaire du Musée zoologique de l'Académie impériale des sciences de St. Pétersbourg 6: 130-164.
- SEAMAN, M. T. & KOK, D. J., VON SCHLICHTING, B. J. & KRUGER, A. J. 1991. Natural growth and reproduction in Triops granarius (Lucas) (Crustacea: Notostraca). Hydrobiologia 212: 87-94.
- SMIRNOV, S. 1936. Zweiter Beitrag zur Phyllopodenfauna Transkaukasiens. Zoologischer Anzeiger 113: 311-320.
- TIWARI, K. K. 1972. Taxonomic status of two recently described Branchiopoda from Kashmir, India. Crustaceana 23: 311-314.
- *VECHOV, N. V. 1988. abronogi /Anostraca /i itni /Notostraca /fauny razlinych prirodnoklimatieskich zon SSSR. Problemy gosudarstvennogo kadastra ivitnogo mira SSSR, sbornik naunych rabot, Moskva 1988, 72–86.
- WILLIAMS, W. D. 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. Hydrobiologia 125: 85-110.
- WILLIAMS, W. D. & BUSBY, J. R. 1991. The geographical distribution of Triops australiensis (Crustacea: Notostraca) in Australia: a biogeoclimatic analysis. Hydrobiologia 212: 235–240.
- WIMAN, F. H. 1979. Mating patterns and speciation in the fairy shrimp genus Streptocephalus. Evolution 33: 172-181.

*-publication not seen.

APPENDIX 1: GAZETEER

Localities from which southern African species of the genus Branchipodopsis were recorded.

| BOISWANA | |
|--------------------------------------|-----------------|
| Gaberone | 24°42'S 25°54'E |
| Gori (Goru?) Pan | 18°S 22°E |
| Kalahari | 20°S 24°E |
| Kanke Pan, 90 miles west of Molepole | 24°24'S 25°32'E |
| Sunnyside | 21°40'S 22°03'E |

| LESOTHO | |
|--|------------------------|
| Brakfontein, 17 km south of Mohale's Hoek | 30°14'S 27°23'E |
| Leloaleng, near Outing | 30°24'S 27°42'E |
| Machoarane Mountain, + 2 km south of Morija (Moraija) | 29°38'S 27°33'E |
| Outward Bound Leribe | 28°58'S 28°09'E |
| Sehlahatehe National Park | 29°50'26"\$ 29°06'52"E |
| | 2) 30 20 8 2) 00 32 1 |
| NAMIBIA | |
| Amichab, 140 km east of Rheboth | 23°13'S 15°32'E |
| Etosha Park | 18°S 14°F |
| Etosha Park Charl Marais (Sukses) Dam | 19°00'32"\$ 15°26'46"F |
| Etosha Park, Leeubron | 19°03'48"\$ 15°48'54"E |
| Great Fish River, near Gibeon | 25°13'S 17°42'E |
| Great Namagualand, Kalkfontain South (Karashurg) | 25 15 5 17 42 E |
| Hereroland West, near Otiituuo | 10°20'S 18°24'E |
| Kaskewald Checkendus, 115 miles north west of Outio | 19 59 5 16 54 E |
| Kaokoveld, Choadendus, 115 miles north-west of Outjo | 19 30 5 15 41 E |
| Kaokoveld, Cauas Okawa | 19°30'S 15°05'E |
| Kaokoveld, Kamanyab | 19-40-8 14-50-E |
| Kaokoveld, Outjo | 20°06'S 16°09'E |
| Kaokoveld, Outjo district, Altmark | 20°06'S 16°09'E |
| Namib Desert, Blutkoppie | 22°48'S 15°22'E |
| Namib Desert, Gemsbokwater, 18 km north of Ganab | 22°56'S 15°37'E |
| Namib Desert, 10 km north-east of Gobabeb, Kuiseb River bed | 23°37'S 15°05'E |
| Namib Desert, near Heinrichsberg | 23°14'S 15°34'E |
| Namib Desert, Mirabib | 23°26'S 15°18'E |
| Namib Naukluft Park, base of Bakenkop | 23°11'S 15°34'E |
| Namib Naukluft Park, 4 km north-north-west of Zebra Pan | 23°31'S 15°28'E |
| Ovamboland, Eunda, ± 100 miles west-north-west of Ondangua | 17°31'S 14°39'E |
| Ovamboland, Onganjera | 17°54'S 15°04'E |
| Waterberg | 20°32'S 17°08'E |
| | |
| SOUTH AFRICA | |
| Cape Province | |
| Amadap Valley | 25°14'S 18°43'E |
| Ashton | 33°49'S 20°03'E |
| Augrabies Falls, Moonrock | 28°35'S 20°19'E |
| Bak River | 28°31'S 17°15'E |
| Bredasdorp, road to Struisbaai | 34°35'S 20°00'E |
| Carnarvon, 10 km south | 31°10'S 22°08'E |
| Eland's Bay | 32°18'S 18°19'E |
| Fraserburg, 8 km north-east | 31°52'S 21°58'E |
| Gordonia, between Keimoes and Upington | 28°30'S 21°14'E |
| Grahamstown | 33°17'S 26°31'E |
| Grahamstown to Cradock road | 33°16'40"S 26°29'05"E |
| Kalahari Gemsbok Park, 40 km south | 26°10'S 20°38'E |
| Karoo, Beaufort West | 32°22'S 22°35'E |
| Karoo, Carnarvon, 10 km south on road to Loxton | 31°10'S 22°08'E |
| Karoo, Fraserburg, 8 km north-east | 31°52'S 21°58'E |

| Karoo, Hoogeveld, south-west of Beaufort West | 33°10'S 21°46'E |
|--|------------------------|
| Karoo, Hutchinson, 30 km south on road to Richmond | 31°30'S 23°29'E |
| Karoo, Williston | 31°20'S 20°50'E |
| Kenton-on-sea | 33°41'S 26°40'E |
| Kimberley | 28°45'S 24°45'E |
| Koppieskraal Pan | 26°56'26"S 20°18'47"E |
| Narugas siding | 28°08'24"S 20°18'47"E |
| Papkuil, near Kimberley | 30°12'S 18°21'E |
| Port Elizabeth | 34°S 25°E |
| Ugie Prentijesberg | 31°09'09"S 28°07'48"E |
| Williston | 31°20'S 20°50'E |
| | 51 20 5 20 50 1 |
| Natal | |
| Drakensberg, Giant's Castle | 29°16'S 29°30'E |
| Drakensberg, Loteni Nature Reserve | 29°26'21"S 29°32'48"E |
| Bushman's Nek/Sehlabatebe Game Reserve border | 19°50'S 29°06'E |
| Drakensberg, Underberg | 29°02'S 29°30'E |
| Drakensberg, Underberg, Bamboo mountain | 29°43'S 29°20'E |
| Umfolozi Game Reserve | 28°17'S 31°49'E |
| Orange Free State | |
| Bloemfontein | 29°07'S 26°14'E |
| Van Reenen, 0.5 miles from | 28°21'S 29°22'E |
| Transvaal | |
| Benoni, Witkoppies | 26°11'S 28°16'E |
| Kruger National Park, Pumbe Pan | 24°10'S 31°55'E |
| Mala Mala Game Reserve | 24°45'S 31°30'E |
| Monane 35 km south of Beit Bridge | 22°36'S 29°52'E |
| Nylsvlei Nature Reserve | 24°39'S 28°42'E |
| ZIMBABWE | |
| Benfer Estates near Umzingwani River | 22°12'\$ 29°56'F |
| Bulawayo | 20°11'S 28°35'E |
| Bulawayo 25 km south-south-west tomb of Phodes | 20°30'00"\$ 28°31'11"E |
| Matanas | 20 50 00 5 20 51 11 E |
| maiopos | 20 JJ 3 20 20 E |